

Can redistribution of breeding colonies on a landscape mitigate changing predation danger?

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The reproductive success of colonially breeding species depends in part upon a trade-off between the benefit of a dilution effect against nestling predation within larger colonies and colony conspicuousness. However, there may be no net survivorship benefit of dilution if smaller colonies are sufficiently inconspicuous. This raises the question about how the size distribution of breeding colonies on a landscape might change as the predation danger for nestlings changes. In southwest British Columbia, Canada, bald eagle *Haliaeetus leucocephalus* populations have increased exponentially at ~5% per year in recent decades and prey upon nestlings of colonial breeding great blue herons *Ardea herodias faninni*. Motivated by field data on reproductive success in relation to colony size, modeling is used to ask under which circumstances trading off a dilution benefit against colony conspicuousness can improve population reproductive success. That is, which colonial nesting distribution, dispersed and cryptic versus clumped and conspicuous, best mitigates predation danger on nestlings? When predators are territorial, the modeling predicts a dispersed nesting strategy as attack rate increases, but not as predator numbers increase. When predators are non-territorial, the modeling predicts a dispersed nesting strategy as predator numbers and/or attack rates increase. When predators are both territorial and non-territorial, colonial nesting within a predator's territory improves reproductive success when attack rates are low. This suggests nesting in association with territorial predators may offer decreased levels of predation when compared with nesting amongst non-territorial predators. Thus a change in the colony size distribution of colonially breeding species might be anticipated on a landscape experiencing a change in predation danger.

The interaction between predation and coloniality has long been debated with many studies suggesting colonial nesting provides benefits over solitary nesting for minimizing predation (e.g. Hamilton 1971, Wittenberger and Hunt 1985, Siegel-Causey and Kharitonov 1990, Danchin and Wagner 1997). Benefits include a dilution effect and/or mobbing behaviour that decreases the probability of colonial nestlings being predated (Hamilton 1971, Turner and Pitcher 1986, Inman and Krebs 1987). Other studies suggest that conspicuous colonial nesting results in an increase in predation rate caused by an increase in predator encounters (Wittenberger and Hunt 1985, Brown and Brown 2001). The location of individuals within a colony (interior versus perimeter) has also been con-

sidered to influence predation danger (Brown and Brown 1987, Brown et al. 1990). Some studies suggest predation is too rare an event to be an important factor influencing colonial nesting (van Vesse and Draulans 1986, Brown and Brown 1987), but the impact of predation must be tested when predation danger to nestlings is significant (Forbes 1989).

Previous theoretical arguments (e.g., Turner and Pitcher 1986, Inman and Krebs 1987) have not examined the relationship between predation risk and coloniality thoroughly enough to understand the predator-prey dynamics affecting reproductive success. As a contribution to understanding coloniality, a theoretical model is presented to illustrate how differing levels of predation may affect the reproductive success of a

colonial nesting bird. Modelling is used to conduct an empirical investigation of population reproductive success for a suite of proposed distributions of colonies and colony sizes on a landscape shared with a particular predator species. The model compares the expected annual reproductive success of a population nesting in various distributions of the number of colonies and colony sizes as the level of predation danger changes (*sensu* Lank and Ydenberg 2003). Predation danger is manipulated by changing the conspicuousness of colonies of different sizes on the landscape, the number of predators on the landscape, the frequency of predatory attacks on nestlings, and the territoriality of the predator. Differences in reproductive success among different distributions of the number of colonies and colony sizes under differing levels of predation danger are discussed in terms of danger mitigation and implications for conservation.

The model is calibrated based upon the Pacific great blue heron *Ardea herodias fannini* – bald eagle *Haliaeetus leucocephalis* predator-prey system. This great blue heron subspecies occurs in southwestern British Columbia and breeds in colonies ranging in size from one to upwards of 400 pairs (Butler et al. 1995). These herons share a productive coastal landscape around the Strait of Georgia with bald eagles, and many studies have reported the bald eagle as a significant predator of heron nestlings (Simpson et al. 1987, Forbes 1987, 1989, Norman et al. 1989, Butler 1992, Vennesland and Butler 2004). Vennesland and Butler (2004) have shown that incursions by bald eagles are the likely reason for all herons in up to 42% of colonies to abandon breeding attempts in a single breeding season.

Over the past few decades, the bald eagle population has increased exponentially at about 5% per year (see Fig. 1) after a decline in the 1950s and 1960s due to

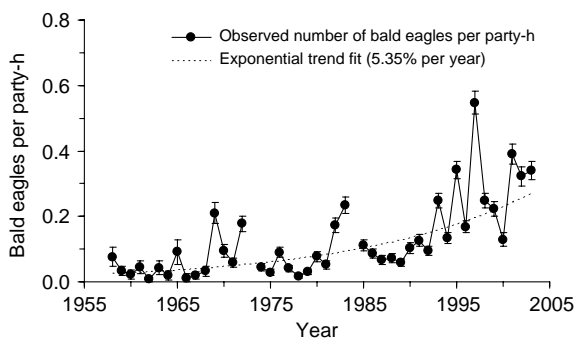


Fig. 1. Index of bald eagle abundance (± 1 SE) near Vancouver, British Columbia, Canada, from 1958 to 2003 using Christmas bird count data from the Vancouver count circle (National Audubon Society 2002). The index for this location shows a similar pattern to indices for adjacent regions.

pesticides and persecution (Buehler 2000, Elliott and Harris 2001). This population increase is concomitant with increased reports of eagle attacks on heron nestlings. Butler and Vennesland (2000) hypothesised that herons may prefer to breed in a more dispersed pattern (i.e., a number of small colonies instead of a single large colony) as a response to this increasing predation danger. Interpretation of additional field data relating reproductive success to colony size supports this possibility. Understanding the mechanism leading to a change in the distribution of colonies on a landscape has important conservation implications since the great blue heron is considered a species of “Special Concern” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2006). The model can inform conservationists of a potential natural change in the distribution of heron breeding colonies in southwestern coastal British Columbia if bald eagles pose an increasing predation threat to heron nestlings.

The predation model

Concept

Imagine a landscape where there are unlimited opportunities for nesting sites, all of equal and high quality. If a population of herons were to be placed on this landscape to breed, then in the absence of nestling predation a nest would be expected to fledge, on average mE nestlings, where m is the proportion of a clutch of size E expected to survive to fledge in the absence of predation. Adult heron mortality during the breeding season is assumed to be negligible.

This model calculates the expected annual reproductive success of simulated populations consisting of N adult heron pairs distributed variously across $c = 1, 2, \dots, C$ colonies on a landscape defined by the number of pairs in each colony c , defined as H_c . The reproductive success of each simulated population is influenced by the level of predation, the length of time (i.e., days in the breeding season) the nestlings are vulnerable to predation (t), and the distribution of colonies of various sizes [H_c]. Pertinent model variables include the total number of heron pairs (N), and the expected number of fledglings per pair in the absence of predation (mE). When predation occurs, the level of predation depends on the number of non-territorial (P_{NT}) and territorial (P_T) eagles present, their daily attack rate upon heron nestlings (A), and the daily probability that an eagle discovers a colony of some size s , ($p[F_s]$). Unlike non-territorial eagles, territorial eagles exclude all other eagles from attacking prey in their territories. The model assumes that eagles are naïve about the location of each year’s newly assembled heron breeding colonies. This assumption is safe since

the largest colonies would be easily found every year, while the smallest colonies, if found, would be depredated or abandoned to re-form elsewhere.

The model's purpose is to express how different distributions of adult herons in breeding colonies differentially mitigate changes in predation danger. The model uses population reproductive success as a measure of predation mitigation calculated from the distribution of breeding pairs (i.e., nests) across colonies on the landscape, for specified values of N , A , E , m , C , H_c , P_{NT} , P_T , t , and $p[F_s]$. Additionally, by adjusting the mix of territorial and non-territorial eagles on the landscape, predation danger can be modified. Though the model can provide an estimate of the reproductive success for a pair of herons for a given set of parameter values, this is not the stated purpose of the model, in part because the model focuses on population level properties.

Values for $p[F_s]$ were calculated by the following submodel:

$$p[F_s] = \beta_0 \left(\frac{1 + e^{-\beta_1(N-\beta_2)}}{1 + e^{-\beta_1(H_c-\beta_2)}} \right) \quad (1)$$

where β_0 is the daily probability of finding a single large colony with N pairs of herons, and β_1 (inflection coefficient) and β_2 (slope coefficient), respectively, determine the location and shape of the detectability relationship between $p[F_s]$ and colony size (conspicuousness). A heron pair's reproductive success is highly sensitive to the parameters of this submodel. For example, the model could assign values of $p[F_s]$ to be equal for all colony sizes such that colony size is irrelevant for being detected by a predator, though predation danger will still vary for individual nests in colonies of different sizes, once they are detected.

Eagles search for heron colonies with a defined probability $p[F_s]$ of finding a colony on any particular day. Once found, eagles randomly depredate nestlings based on the attack rate A and the uniform probability of finding a surviving nestling among the remaining active nests within that colony. When more than one colony is available to an eagle, colonies are depredated sequentially until the end of the breeding season of length (t). Specifically, an eagle randomly selects an individual nest (n) in a previously unpredated colony according to:

$$p[F_n] = \frac{1}{H_c}, \quad (2a)$$

then a nestling is randomly depredated from that nest. After each predation event, the model updates population reproductive success by subtracting one nestling from both R_n and R_c , where $R_c = mEH_c$ is the reproductive success of the colony before any depredation and R_n is the remaining number of nestlings in any

nest n . Each time a nest is completely depredated the revised probability of a nest being attacked is determined by:

$$p[F_n] = \frac{1}{H_c - \left(\sum_{n=1}^{H_c} I_n \right)} \quad (2b)$$

where

$$I_n = \begin{cases} 0 & \text{if } R_n = 0 \\ 1 & \text{if } R_n > 0 \end{cases} \quad (2c)$$

Eagles show no preference for nests based on the number of surviving nestlings when $R_n > 0$. Each day, eagles continue to take nestlings until the colony is completely depredated or they reach their daily attack rate A . At the end of the herons' breeding season the performance of the heron population is measured in terms of the average reproductive success per nest (\bar{R}_N) where:

$$\bar{R}_N = \frac{\sum_{n=1}^N R_n}{N} \quad (3)$$

Model's application to field data

The motivation for pursuing this work followed from scrutiny of field data collected adjacent to the Strait of Georgia from 1988 to 1992 on the reproductive success of great blue heron colonies in relation to colony size (see Butler et al. 1995, Moul et al. 2001), and a similar assessment in 1999 by Vennesland and Butler (2004). Two statistical features of these data led to the suspicion that, notwithstanding colony abandonment, both colony size and conspicuousness potentially affected the reproductive success of individual nests. As shown in Fig. 3a, (1) mean reproductive success per nest tends to increase as colony size increases, and (2) the standard deviation (SD) of reproductive success per nest decreases with increasing colony size. With respect to (2), smaller colonies were more characterised by nests that either completely failed, or fledged all chicks, than were larger colonies in which individual nests tended to have a reproductive success near the mean.

The predation model described above was designed to explain the patterns of mean reproductive success and SD of reproductive success observed in the field data (Fig. 3a) using the simplest rational concept for the predator-prey relationship between eagles and heron nestlings. That concept incorporated three basic premises (1) eagles can be territorial or non-territorial, (2) herons breed in colonies of various sizes, and (3) there is potentially a large difference in the conspicuousness to

eagles of the smallest (e.g., one nest) to the largest (e.g., several hundred nests) colonies. This latter concept of conspicuousness is quantified in Eq. 1, and portrayed in Fig. 2, where the difference in conspicuousness of small and large colonies is referred to as “contrast”.

Since the field data are an incomplete representation of heron distribution on the landscape, and no unique set of model parameters would explain them, the purpose in analyzing them was solely to judge if a trade-off of colony size and conspicuousness was an *a priori* plausible explanation for the field data. Therefore, the predation model was fitted to the observed field data using the following protocol. First, a distribution of heron colonies on a landscape was defined using the field data (i.e., values for N , H_c , C , Table 1). Then a search was performed for values of P_T , A , and m , as well as for parameters of Eq. 1 (β_0 , β_1 , β_2), corresponding to a strong contrast, and two “no contrast”, scenarios with respect to the daily probability of finding a colony of a particular size ($p[F_s]$). For each set of model parameters 1024 breeding season predation simulations were performed to provide a confident estimate of the mean and SD of reproductive success per nest for each colony size. Additionally, a null scenario with no eagle attacks was included.

Model’s application to simulated landscape

The analysis of field data addressed only the plausibility that colony size and conspicuousness affected reproductive success for a single colony size distribution. To

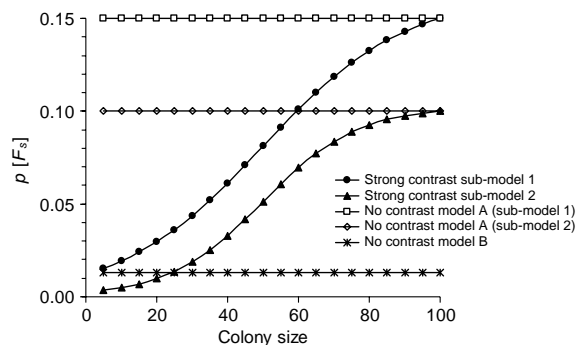


Fig. 2. Relationships between the daily probability with which a colony is found by an eagle, $p[F_s]$, and colony size, H_c . Relationships are presented for three models defined by the function in Eq. 1. In the strong contrast model large colonies are much more likely to be found by an eagle than are small colonies. This circumstance is represented by strong contrast sub-model 1 and strong contrast sub-model 2. Two models use a relationship where all colonies have the same probability of being found. That probability is relatively high (0.15 in sub-model 1 or 0.10 in sub-model 2) in one circumstance (no contrast model A), and relatively low in the other (no contrast model B).

compare the estimated reproductive success among various distributions of colonies representing different conceivable levels of predation danger, the model allowed heron pairs to nest in a diverse set of unique colony distributions. Mathematically, each member of this set of distributions is known as a partition (ρ) of N . There are as many partitions of N as there are ways that the distribution of N heron pairs among the C colonies can be arranged. For $N = 100$, as chosen for this study, the two extreme partitions are 100 colonies of one (1) pair (nest) each, or one (1) colony of 100 pairs, where the number of all possible partitions of $N = 100$ is the impractically large number 190,569,292. This numerical constraint was overcome by restricting colony sizes to be a multiple of five; thereby resulting in a maximum of $\frac{N}{5} = 20$ colonies. This yielded the more practical value of 627 partitions, with a colony of five heron pairs as the smallest possible (H_{min}).

The model identifies the colony distribution at different levels of predation danger that maximizes reproductive success for the entire population. The level of predation danger is determined from the per capita daily number of attacks on nestling herons, A , and the number and behaviour (territorial or non-territorial) of eagles. Allowing the daily predation rate to change reflects possible specialization of eagles on heron nestlings. At the landscape level, eagle territoriality at one extreme consists of P_T territorial eagles whose randomly assigned exclusive territories include all colonies of a particular partition. In this scenario non-territorial eagles are irrelevant since they cannot encroach on the landscape defended by a territorial eagle ($P_{NT} = 0$). The opposite scenario occurs when all eagles are non-territorial, each heron colony being susceptible to an attack from any eagle ($P_T = 0$ and $P_{NT} > 0$). A third scenario looked at a combination of territorial and non-territorial eagles where P_T territorial eagles defend their own unique heron colony from all other eagles while non-territorial eagles were allowed to search for and attack any and all heron colonies not under protection from a territorial eagle. This scenario may be considered analogous to a situation where breeding adult eagles hold a territory and a population of non-territorial juvenile eagles are on the same landscape. For this last scenario, the model only used the value of P_{NT} equal to four (4) eagles since values of $P_{NT} > 4$ produced qualitative results very similar to when $P_{NT} = 4$. Values of $P_{NT} < 4$ produced qualitative results that were between the results obtained when $P_{NT} = 4$ and results obtained when only territorial eagles occurred.

Each distribution (partition) was executed using the fixed values of $N = 100$, $E = 4$, $m = 1$, $C = 20$, and $t = 50$ days, while values for P_{NT} , P_T , the vector of values of H_c , and the mix of territorial and non-territorial

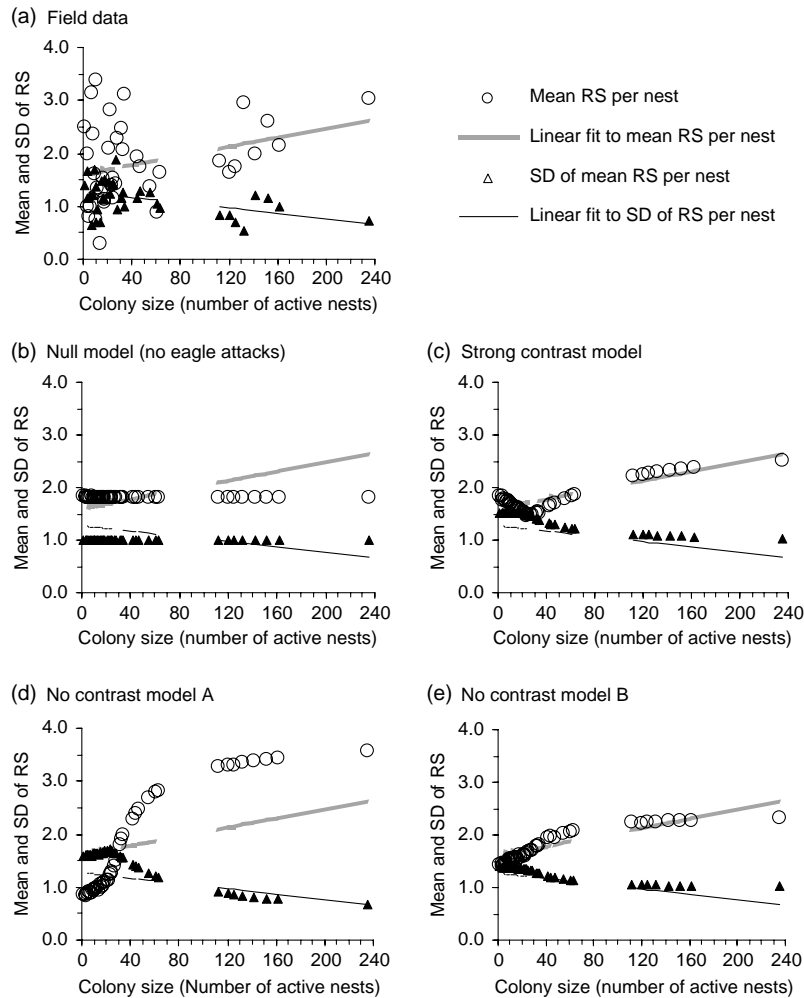


Fig. 3. Predation model fits to 1988 to 1992 field data portraying the relationship between colony size and the mean and SD of reproductive success (RS) per nest. As a baseline for comparison of the competing predation models, observed data for the mean (large open circles) and SD (solid black triangles) of reproductive success are first fit by simple linear regression in panel a ($r^2 = 0.11$). Panels b–d then compare the fits of four proposed predation models for the mean and SD of reproductive success per nest. Panel b portrays a null model with no predation ($r^2 = 0.00$), while panel c (strong contrast model) portrays a steep decrease in colony conspicuousness ($p[F_s]$) as colony size decreases ($r^2 = 0.61$); see Fig. 2. Panel d (no contrast model A) portrays equal but relatively high conspicuousness of colonies of all sizes ($r^2 < 0$), while panel e (no contrast model B) portrays equal but relatively low conspicuousness of colonies of all sizes ($r^2 = 0.66$); see Fig. 2. Values for r^2 for panels d–e refer to the predation model fits to the linear fit for mean RS per nest. The value for $r^2 < 0$ for no contrast model A indicates that this model fit more poorly than the null model (panel b) with no predation.

eagles was varied to simulate different levels of predation danger. Unlike the model's application to field data, here it is assumed $m = 1$ since model results are qualitatively insensitive to random mortality unrelated to the distribution of colonies on the landscape.

Models were run for the three predator landscape scenarios described above to evaluate two alternate hypotheses (strong contrast versus no contrast) regarding the conspicuousness of heron colonies of different sizes. The first evaluation assumed that larger colonies are considerably more conspicuous than smaller colo-

nies and therefore easier for predators to find. This "Strong Contrast Model" uses parameter values associated with the Fig. 3c fit to the field data. The strength of this relationship between colony size (s) and $p[F_s]$ is exemplified in Fig. 2 where it is compared to two "no contrast" models. Two Strong Contrast sub-models are used (Fig. 2) since strong contrast sub-model 1 led to complete depredation of nestlings in some simulations with non-territorial eagles. The two "no contrast" models assume there is no relative difference in detectability among colonies of different sizes, colonies

Table 1. Parameter values for the predation model fits to 1988 to 1992 field data (Fig. 3c, d, e). In all cases the predator is a territorial eagle.

Symbol	Definition	Values		
		Strong contrast model Fig. 3c	No contrast model A Fig. 3d	No contrast model Fig. 3e
N	Number of nests	2591	2591	2591
P_T	Number of territorial eagles	76	76	76
A	Daily attack rate	2	2	2
E	Clutch size	4	4	4
m	Non-predatory chick survival rate to t	0.70	0.60	0.96
C	Maximum number of colonies	76	76	76
$H_{min}; H_{max}$	Minimum; maximum colony size	1;235	1;235	1;235
t	Number of provisioning days	50	50	50
β_0	$p[F_s = N]$	0.162	0.162	0.013
β_1	Slope coefficient	0.05	0	0
β_2	Colony size at inflection	50	50	50

differing only in their constant value of $p[F_s]$. In “No Contrast Model A”, motivated by Fig. 3d, $p[F_s]$ was set to a relatively large value (0.15 in sub-model 1 or 0.10 in sub-model 2) for all C colonies (Table 2). Once again, to prevent complete depredation of nestlings in some simulations with non-territorial eagles, $p[F_s]$ was set to 0.15 in sub-model 1 and 0.10 in sub-model 2. In “No Contrast Model B”, motivated by Fig. 3e, $p[F_s]$ was set to a relatively small value (0.013). For all models, a matrix of values of eagle number and daily

predation rate per eagle is used to define the varying levels and combinations of predation danger.

Presentation of output

Each partition is ranked by increasing SD of the partition (SD_p) on a colony size dispersion index ranging from a partition that is termed ‘clumped’ (a single large colony, low SD of dispersion in colony size)

Table 2. Parameter values for three alternate models of colony conspicuousness and size. For the strong contrast model larger colonies have a much higher daily probability ($p[F_s]$) of being detected by a predator than smaller colonies, while colonies of all sizes have the same daily probability ($p[F_s]$) of being detected in no contrast model A and no contrast model B. Column subheadings “Territorial”, “Territorial and Non-territorial”, and “Non-territorial” refer to the behaviour of the eagles included in the model.

Symbol	Definition	Values		
		Territorial	Territorial and Non-territorial	Non-territorial
		All models		
N	Number of nests	100	100	100
E	Clutch size	4	4	4
m	Non-predatory chick survival rate to t	1.00	1.00	1.00
C	Maximum number of colonies	20	20	20
$H_{min}; H_{max}$	Minimum; maximum colony size	5;100	5;100	5;100
t	Number of provisioning days	50	50	50
A	Daily attack rates	1,2,4,8,16,32	1,2,4,8,16,32	1,2,4,8,16,32
P_T	Number of territorial eagles	1,2,4,8,12,16,20	1,2,4,8,12,16,20	0
P_{NT}	Number of non-territorial eagles	0	4	1,2,4,8,12,16,20
β_2	Colony size at inflection	50	50	50
		Strong contrast model		
β_0	$p[F_s = N]$	Fig. 4a 0.15	Fig. 4b 0.15	Fig. 4c 0.10
β_1	Slope coefficient	0.05	0.05	0.075
		No contrast model A		
β_0	$p[F_s = N]$	Fig. 4d 0.15	Fig. 4e 0.10	Fig. 4f 0.10
β_1	Slope coefficient	0	0	0
		No contrast model B		
β_0	$p[F_s = N]$	Fig. 4g 0.013	Fig. 4h 0.013	Fig. 4i 0.013
β_1	Slope coefficient	0	0	0

to one termed ‘dispersed’ (20 small colonies, high SD of dispersion in colony size). Values for SD_p are calculated from the distribution of colony sizes across colony number, where colonies are sequentially and arbitrarily numbered from $c = 1$ to C , with mean (μ_p)

$$\mu_p = \frac{\sum_{c=1}^C cH_c}{N}, \quad (4)$$

and SD

$$SD_p = \sqrt{\left(\frac{\sum_{c=1}^C c^2 H_c}{N} - \mu_p^2 \right)}. \quad (5)$$

Thus, if $N = 100$ herons are in a single colony, $C = 1$, then $SD_p = 0$, whereas if $N = 100$ herons are dispersed evenly across $C = 20$ colonies, all $H_C = 5$, then SD_p is maximized ($SD_p = 5.766$). Note that though μ_p is dependent upon the arbitrary ordering of colony sizes, SD_p is not order dependent.

For a given set of parameter values (eagle number, attack rate, etc.), the slope (γ) of the linear relationship between the average reproductive success (\bar{R}_N) and the dispersion index (SD_p) is used to describe the performance of clumped versus dispersed nesting strategies for a given level of predation danger. Increasingly positive slopes suggest that an increasingly dispersed nesting strategy best mitigates predation danger whereas increasingly negative slopes suggest that a more clumped nesting strategy best mitigates predation danger. If the slope is zero there is no difference in reproductive success among all nesting strategies. This latter result can occur via three mechanisms: (1) very little predation, (2) some predation, but at the same level for all distributions, or (3) a large amount of predation causing reproductive success to approach zero for all distributions. Surface plots (Fig. 4) showing the value of the slope (γ) for each combination of eagle number and daily attack rate display the trend of nesting distributions that best mitigate the differing levels of predation danger.

Results

Field data

Modelling validates that a plausible explanation for the trends in the mean and SD of reproductive success is variability in the conspicuousness and size of colonies (Fig. 3). Both strong contrast (Fig. 3c) and no contrast with a low $p[F_s]$ (Fig. 3e) reasonably explain the observed data. In all cases the model slightly overestimates the

observed SD of reproductive success (which in the model is defined by the binomial mortality process). The overestimated SDs suggest that herons may be behaving to reduce the otherwise random variance in reproductive success. Though modeling suggests that the field data could be explained by a process where $p[F_s]$ is small and does not vary with colony size (Fig. 3e), this explanation does not incorporate the reality on the landscape that large and noisy colonies, perhaps with 100 or more nests, are obviously more conspicuous than dispersed, small, cryptic colonies of one to a few nests.

Strong contrast model

Eagle territoriality has a large influence on the nesting distribution that best mitigates predation danger. For “territorial eagles only”, Fig. 4a shows that the number of eagles has little effect on the nesting distribution that best mitigates danger. However, as the level of predation danger increases through an increase in the daily attack rate, A , the population reproductive success increases under a more dispersed nesting distribution. The preference for a clumped nesting distribution rather than a dispersed nesting distribution occurs as the dilution effect breaks down, causing nesting in large colonies to become a poor option due to the conspicuousness of the colony to predators. Adding non-territorial eagles to the model predicts that increasing eagle numbers could lead to a more dispersed nesting distribution (Fig. 4b). As the predation rate increases population reproductive success is highest when the nesting distribution is several small colonies, similar to “territorial eagles only”. With few territorial eagles and low daily predation rates, the surface plot suggests a clumped nesting distribution increases reproductive success, possibly due to herons paying a small price, in terms of lost reproduction, to a territorial eagle in an attempt to avoid predation by the many non-territorial eagles. “Non-territorial eagles only” (Fig. 4c) yields similar predictions. A more dispersed nesting distribution improves population reproductive success as predation danger increases but only up to a point before the trend is reversed (Fig. 4c). This reversal is due to overall predation being so high that it reduces the reproductive success of the herons to zero, creating the appearance, legitimately, of no unique distribution that best mitigates predation danger.

No contrast models

Models where all colonies have an equal probability of being found, regardless of their size, suggest that colony detectability is an important factor determining the reproductive success of different colony distributions. There is little difference between “territorial eagles

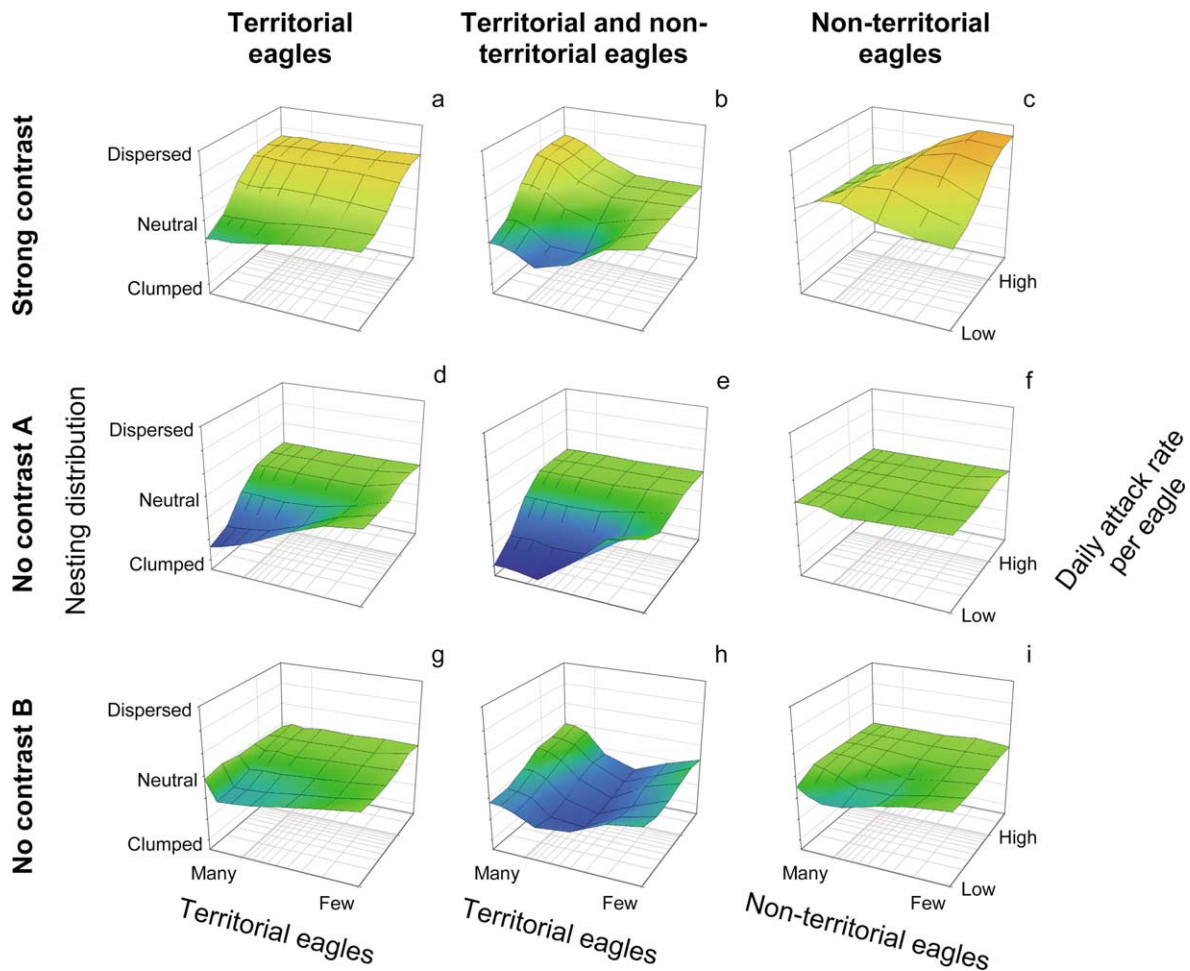


Fig. 4. Different levels of predation danger (number of eagles and their attack rate) lead to different nesting distributions (i.e., clumped versus dispersed, γ) that best mitigate that danger (i.e., maximize reproductive success). Predation danger is measured by the number of territorial or non-territorial eagles (log scale) and the potential daily attack rate per eagle (log scale). Panels a–i portray nesting distributions that best mitigate danger for different predator-prey landscapes. (Details for each plot are cross-referenced in Table 2). Dark blue identifies where a clumped nesting distribution best mitigates danger; orange identifies where a dispersed nesting distribution best mitigates danger; and light green indicates where neither a clumped nor dispersed distribution is more beneficial for danger mitigation, perhaps due to extremely low or high predation mortality.

only” and “territorial and non-territorial eagles” in “No Contrast Model A” (Fig. 4d, e), where a colony’s probability of being found is relatively high. In both of these cases, a clumped distribution of heron colonies seems to best mitigate predation danger, with the mitigation of predation danger increasing at higher territorial eagle numbers. As the predation rate increases to excessive levels, no nesting distribution outperforms other nesting distributions in terms of mitigating predation danger due to reproductive success being close to zero for all nesting distributions. “Non-territorial eagles only” under the “No contrast model A” yields predation levels so high for all combinations

of eagle abundance and attack rate that the reproductive success approaches zero and the response surface of γ ’s is neutral (Fig. 4f).

When eagles find all colonies with the same, but relatively low, probability (“No Contrast Model B”), the results are similar to those found in the “strong contrast model” when territorial eagles are present in some manner (Fig. 4g, h). Fig. 4i is similar to Fig. 4f, suggesting that the numerical value of the probability of a colony being discovered by an eagle under a no contrast scenario is irrelevant. The three models with non-territorial eagles (Fig. 4c, f and i) suggest that if predators are not territorial then dispersed nesting could

effectively mitigate danger only when there is a strong contrast in the probabilities of finding colonies of different sizes.

Discussion

The formal predator-prey model presented here has shown why prior verbal models have reached the contradictory conclusions that increasing (Hamilton 1971, Wittenberger and Hunt 1985, Siegel-Causey and Kharitonov 1990, Danchin and Wagner 1997), or decreasing (Wittenberger and Hunt 1985, Brown and Brown 2001) colony size will mitigate changes in predation rate. As shown here by modelling and comparing two contrasting assumptions of colony detectability with respect to colony size, the difference in the detection probabilities of large and small colonies can be the key factor leading to different predictions. A difference in the probability of colony detection has been proposed in the literature as a rationale for large colonies (Wittenberger and Hunt 1985) but this idea had not been tested with a particular predator-colonial nesting prey system. However, Cresswell (1994) found larger groups of non-breeding birds experienced a higher frequency of predatory attacks. When small and large colonies are equally detectable, small colonies are predicted to be unable to mitigate increases in predation danger compared to colonies where detection probability increases as colony size increases (see Fig. 4a, b, d, e, g, and h).

Most of the territorial scenarios used in this study predict a trend toward a more dispersed nesting distribution to mitigate predation danger. However, Fig. 4b and h suggest a clumped nesting distribution may be most beneficial despite an increase in predation danger. In this situation, herons may deliberately nest in association with a territorial eagle to reduce predation from non-territorial eagles. Nesting in association with a territorial predator can be beneficial when the alternative is increased predation from other predators. Nesting associations between a colonial nesting species and a territorial predator, or at least an aggressive territorial species, have previously been documented in a number of colonial nesting species (e.g., Bogliani et al. 1999, Quinn et al. 2003). Bald eagles have been observed nesting in association with large heron colonies in southwestern British Columbia.

Field tests of the hypothesis that nesting distributions will change when predation danger increases are difficult to execute. Hogstad (1995) found a positive correlation between the number of fieldfare *Turdus pilaris* colonies and the abundance of rodents. When the rodent population size declined to extremely low numbers, their main predator (mustelids) switched to preying upon fieldfares. An increase in danger was

suggested to cause a shift in fieldfare nesting distribution from colonial to solitary in years when the rodent population was low. Wiklund and Andersson (1994) found the presence of tawny owls *Strix aluco* in southern Sweden to be correlated with smaller colonies of fieldfares when compared with northern Sweden where the owls were absent. Similarly, Quinn and Kokorev (2002) found colonial breeding red-breasted geese *Branta ruficollis* to abandon their nests when lemming populations were low and when their nesting associate, the peregrine falcon *Falco peregrinus*, increased its aggressive behaviour. This occurred despite the benefit falcons provide for deterring other goose predators. Many studies have suggested correlations of predation danger with degree of colonial nesting. Clode (1993) claims seabirds tend to nest solitarily or in small colonies in highly dangerous inshore habitats, and are more likely to nest in larger colonies in less dangerous offshore habitats, consistent with the predictions in this study. Most studies have attempted to determine only if the probability of predation is greater inside or outside a colony (e.g., Andersson and Wiklund 1978, Bellinato and Bogliani 1995) rather than varying the degree of danger in the environment.

The present model's precise predictions will differ from those of a stochastic dynamic model that assesses the fitness and colony size choice decisions of individual herons, though they should be qualitatively similar. For example, Sibly (1983) predicts observed group sizes to be larger than the theoretically optimal group size because individuals in poorly performing groups would increase their fitness by joining a group that is already at the optimal size. With reference to the model presented here, the argument would be that the distribution of colonies and colony sizes that maximizes population reproductive success for a particular level of danger would most likely be maximized at less than the highest values for population reproductive success. Additionally, several hypotheses have been proposed that describe factors other than predation that determine the size of colonies. These include food-finding benefits (e.g. Ward and Zahavi 1973, Krebs 1974), hidden leks (Draulans 1988, Morton et al. 1990, Wagner 1993), proximity to food sources (Sergio et al. 2003) and conspecific reproductive success (Danchin et al. 1998). The role any of these hypotheses might play in colonial nesting has not been addressed here.

One key value of the predictions made by this model is guidance for conserving this colonial nesting species. The Pacific great blue heron population in southwestern British Columbia is listed as a species of "Special Concern" (COSEWIC 2006), in part due to the frequent abandonment of breeding attempts by entire colonies (Vennesland and Butler 2004). Conservation measures have included enacting and enforcing laws that protect heron colonies from human

disturbance during the breeding season and protecting a few extant large colonies by purchasing the land on which they occur. This latter action reflects a, perhaps outdated, belief that these heron colonies are likely to persist at that location.

As raptor numbers rebound from persecution and pesticides (Buehler 2000), changes in the distribution and size of breeding colonies can be anticipated for many prey species as a possible response to increases in predation danger. Depending upon the territoriality of the eagles, nesting associations which are occasionally seen with large colonies, may become a more common feature of heron breeding colonies. Alternatively, the model presented here challenges the idea that large colonies will persist at their contemporary locations and suggests that a more dispersed nesting distribution may best mitigate predation danger. That is, the landscape may be becoming more dangerous for individual herons nesting in conspicuous large colonies as the danger of eagle predation increases, especially from non-territorial eagles. Thus the contemporary conservation practice of protecting individual colonies may not be effective in the future since herons may require a landscape offering flexibility of choice for the location and size of their breeding colonies.

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References

- Andersson, M. and Wiklund, C. G. 1978. Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). – *Anim. Behav.* 26: 1207–1212.
- Bellinato, F. and Bogliani, G. 1995. Colonial breeding imposes increased predation: experimental studies with herons. – *Ethol. Ecol. Evol.* 7: 347–353.
- Bogliani, G., Sergio, F. and Tavecchia, G. 1999. Woodpeckers nesting in association with hobby falcons: advantages and choice rules. – *Anim. Behav.* 57: 125–131.
- Brown, C. R. and Brown, M. B. 1987. Group-living in cliff swallows as an advantage in avoiding predators. – *Behav. Ecol. Sociobiol.* 21: 97–107.
- Brown, C. R. and Brown, M. B. 2001. Avian coloniality: progress and problems. – In: Nolan, V., Jr. and Thompson, C. F. (eds). *Curr. Ornithol.*, vol. 16. Plenum, New York, pp. 1–82.
- Brown, C. R., Stutchbury, B. J. and Walsh, P. D. 1990. Choice of colony size in birds. – *Trends Ecol. Evol.* 5: 398–403.
- Buehler, D. A. 2000. Bald eagle (*Haliaeetus leucocephalus*). – In: Poole, A. and Gill, F. (eds). *The birds of North America*, no. 506. The birds of North America, Inc., Philadelphia, PA.
- Butler, R. W. 1992. Great blue heron. – In: Poole, A. P., Stettenheim, P. and Gill, F. (eds). *The birds of North America*, no. 25. The birds of North America, Inc., Philadelphia, PA.
- Butler, R. W., Whitehead, P. E., Breault, A. M. and Moul, I. E. 1995. Colony effects on fledging success of great blue herons (*Ardea herodias*) in British Columbia. – *Colon. Waterbirds* 18: 159–165.
- Butler, R. W. and Vennesland, R. G. 2000. Integrating climate change and predation risk with wading bird conservation research in North America. – *Waterbirds* 23: 535–540.
- Clode, D. 1993. Colonially breeding seabirds: predators or prey? – *Trends Ecol. Evol.* 8: 336–338.
- COSEWIC. 2006. Canadian species at risk. – Committee on the status of endangered wildlife in Canada (COSEWIC). Web site: http://www.cosewic.gc.ca/eng/sct0/rpt/rpt_csar_e.cfm.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. – *Anim. Behav.* 47: 433–442.
- Danchin, E. and Wagner, R. H. 1997. The evolution of coloniality: the emergence of new perspectives. – *Trends Ecol. Evol.* 12: 342–347.
- Danchin, E., Boulinier, T. and Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. – *Ecology* 79: 2415–2428.
- Draulans, D. 1988. The importance of heronries for mate attraction. – *Ardea* 76: 187–192.
- Elliott, J. E. and Harris, M. L. 2001. An ecotoxicological assessment of chlorinated hydrocarbon effects on bald eagle populations. – *Rev. Toxicol.* 4: 1–60.
- Forbes, L. S. 1987. Predation on adult great blue herons: is it important? – *Colon. Waterbirds* 10: 120–122.
- Forbes, L. S. 1989. Coloniality in herons: Lack's predation hypothesis reconsidered. – *Colon. Waterbirds* 12: 24–29.
- Hamilton, W. D. 1971. Geometry for the selfish herd. – *J. Theor. Biol.* 31: 295–311.
- Hogstad, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of fieldfares *Turdus pilaris*? A 15-year study. – *Ibis* 137: 484–489.
- Inman, A. J. and Krebs, J. R. 1987. Predation and group living. – *Trends Ecol. Evol.* 2: 31–32.
- Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). – *Behaviour* 51: 99–134.
- Lank, D. B. and Ydenberg, R. C. 2003. Death and danger at migratory stopovers: problems with "predation risk". – *J. Avian Biol.* 34: 225–228.
- Morton, E. S., Forman, L. and Braun, M. 1990. Extrapair fertilizations and the evolution of colonial breeding in purple martins. – *Auk* 107: 275–283.
- Moul, I. E., Vennesland, R. G., Harris, M. L. and Butler, R. W. 2001. Standardizing and interpreting nesting records for great blue herons in British Columbia. – Canadian wildlife service progress note no. 217, Canadian wildlife service, Ottawa.

- National Audubon Society, 2002. The Christmas bird count historical results [Online]. – Available at: <http://www.audubon.org/bird/cbc>.
- Norman, D. M., Breault, A. M. and Moul, I. E. 1989. Bald Eagle incursion and predation at great blue heron colonies. – *Colon. Waterbirds* 12: 215–217.
- Quinn, J. L. and Kokorev, Y. 2002. Trading-off risks from predators and from aggressive hosts. – *Behav. Ecol. Sociobiol.* 51: 455–460.
- Quinn, J. L., Prop, J., Kokorev, Y. and Blacks, J. M. 2003. Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum. – *Anim. Behav.* 65: 297–307.
- Sergio, F., Marchesi, L. and Pedrini, P. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. – *J. Anim. Ecol.* 72: 232–245.
- Sibly, R. M. 1983. Optimal group size is unstable. – *Anim. Behav.* 31: 947–948.
- Siegel-Causey, D. and Kharitonov, S. P. 1990. The evolution of coloniality. – In: Power, D. M. (ed.). *Curr. Ornithol.*, vol 7. Plenum, New York, pp. 285–330.
- Simpson, K., Smith, J. N. M. and Kelsall, J. P. 1987. Correlates and consequences of coloniality in great blue herons. – *Can. J. Zool.* 65: 572–577.
- Turner, G. F. and Pitcher, T. J. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. – *Am. Nat.* 128: 228–240.
- van Vessem, J. and Draulans, D. 1986. The adaptive significance of colonial breeding in the grey heron *Ardea cinerea*: inter- and intra-colony variability in breeding success. – *Ornis Scand.* 17: 356–362.
- Vennesland, R. G. and Butler, R. W. 2004. Factors influencing great blue heron nesting productivity on the Pacific coast of Canada from 1998 to 1999. – *Waterbirds* 27: 289–296.
- Wagner, R. H. 1993. The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. – *J. Theor. Biol.* 163: 333–346.
- Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. – *Ibis* 115: 517–534.
- Wiklund, C. G. and Andersson, M. 1994. Natural selection of colony size in a passerine bird. – *J. Anim. Ecol.* 63: 765–774.
- Wittenberger, J. F. and Hunt, G. L. Jr. 1985. The adaptive significance of coloniality in birds. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds). *Avian biology*, vol 8. Academic Press, London, pp. 1–78.