Risk perception of nesting Great Blue Herons: experimental evidence of habituation

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Abstract: The nesting behaviour of the Great Blue Heron (*Ardea herodias* L., 1758) was studied in western Canada in 1998 and 1999 to (*i*) investigate how individual parents assess risk when repeatedly exposed to a disturbance stimulus (an investigator) and (*ii*) experimentally test in the field whether any variation in their nest defense behaviour was due to experience with the disturbance stimuli or the stage of the nesting period. Heron response declined through the nesting period and the level of response varied among colonies, suggesting different perceptions of risk among groups of herons in the study. It was experimentally shown that variation in the response of herons through one nesting period was due to both behavioural habituation and the stage of the nesting period. Response was stronger in 1999 than in 1998, indicating that habituation did not hold between nesting periods. In general, habituation in herons may bode well for their potential to persist in areas with light human use. But irrespective of habituation, stimuli early in the nesting period and large or novel events may still cause herons to abandon their nests owing to the effects of the stage of the nesting period.

Résumé : Le comportement de nidification du grand héron (*Ardea herodias* L., 1758) a été examiné dans l'Ouest canadien en 1998 et 1999 afin (*i*) d'étudier comment les parents individuels évaluent le risque lorsqu'ils sont exposés à répétition à un stimulus de perturbation (présence d'un chercheur) et (*ii*) de vérifier expérimentalement en nature si la variation de leur comportement de défense du nid est due à leur expérience vis-à-vis le stimulus de perturbation ou au stade de la période de nidification. Les réactions des hérons diminuent au cours de la période de nidification et l'importance de la réaction varie d'une colonie à l'autre, ce qui indique qu'il y a des différences de perception des risques parmi les groupes de hérons à l'étude. Des expériences montrent que la variation des réactions des hérons au cours d'une période de nidification est due tant à l'habituation comportementale qu'au stade de la période de nidification. Les réactions ont été plus fortes en 1999 qu'en 1998, ce qui indique que l'habituation ne se maintient pas d'une période de nidification à l'autre. En général, l'habituation chez les hérons est un signe encourageant pour le potentiel de persistance des hérons dans les zones de faible utilisation humaine. Mais malgré l'habituation, des stimuli tôt dans la période de nidification et des événements importants ou inédits peuvent encore amener les hérons à abandonner leur nid à cause des effets associés au stade de la période de nidification.

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Introduction

The defense of offspring at the nest is an important component of parental care in birds because of the strong influence predators exert on nesting productivity (Ricklefs 1969; Montgomerie and Weatherhead 1988; Lima and Dill 1990). Naturalists have long observed changes in nest defense by birds through the nesting period (e.g., Simmons 1955), and much effort has gone into understanding the adaptive significance of these changes in behaviour (reviewed by Montgomerie and Weatherhead 1988).

Many studies have shown that parent birds risk injury or death when mobbing or displaying to predators (Montgomerie and Weatherhead 1988), and nesting success has been positively correlated with the intensity of nest defense (Andersson et al. 1980; Greig-Smith 1980; Blancher and Robertson 1982; Knight and Temple 1986; Breitwisch 1988). Parental fitness can be influenced directly from the death of nesting adults or the brood, or indirectly through a reduction in the energy available for growth or further reproduction because of the cost of defense responses (Magnhagen 1991; Stearns 1992; Lima 1998). Because of such potential fitness costs, parents should adjust their level of defense to match the seriousness of the threat (Ydenberg and Dill 1986; Lima and Dill 1990).

Active nest defense, such as mobbing predators, is uncommon for Great Blue Herons (*Ardea herodias* L., 1758), likely because they are too large to effectively harass smaller and more manoeuvrable predators (Burger 1981; Forbes 1989) and are at risk themselves to larger predators (Forbes 1987; Butler 1997). Nesting herons in south-coastal British Columbia are regularly attacked by Bald Eagles (*Haliaeetus leucocephalus* (L., 1766)) that prey mostly on eggs and nestlings (Norman et al. 1989; Vennesland and Butler 2004) and rarely on adults (Forbes 1987; Butler 1997). Adults are rarely killed at the nest because they frequently flush from nests during attacks by eagles (Vennesland and Butler 2004). This response leaves the adult safe but the nest contents vulnerable. Thus, heron nest defense is

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best described as staying at the nest as long as possible as a potential predator approaches (i.e., not advertising the nest contents). Without addressing the underlying endocrine mechanism involved (e.g., Walker et al. 2006), the distance at which a heron responds to an approaching disturbance stimulus (in this case, an approaching human pedestrian) provides a gauge of the sensitivity of nesting herons and a relative measure of the trade-off between risk to the parent and risk to the brood required for investigations into parental nest defense behaviour (Montgomerie and Weatherhead 1988). Forbes et al. (1994) and Gunness and Weatherhead (2002) used a similar perspective when investigating the nest defense behaviour of several species of waterfowl to investigator disturbance.

The objectives of this study were to (*i*) determine whether Great Blue Herons alter their nest defense behaviour to the repeated and standardized approach of an investigator within and between nesting periods and (*ii*) experimentally test in the field for behavioural flexibility in the response from Great Blue Herons to this disturbance stimulus, specifically to assess whether and how they habituate.

One rationale for this study was to investigate the methodological implications of repeated presentations of an ultimately nonthreatening disturbance stimulus to nesting birds. Studies of avian nest defense behaviour have shown that parent birds can respond flexibly to repeated and ultimately nonthreatening disturbance stimuli (reviewed by Montgomerie and Weatherhead 1988). Research has found that parental experience had no effect (Redondo and Carranza 1989; Weatherhead 1989; Westneat 1989) or an amplifying effect (Forbes et al. 1994; Gunness and Weatherhead 2002) on response. Knight and Temple (1986) predicted that parent birds should reduce their response (i.e., habituate) to repeated presentations of an ultimately nonthreatening disturbance stimulus, and pointed out that habituation has the potential to confound conclusions about the characteristics of nest defense because both habituation and factors based on the stage of the nesting period (e.g., the value of the brood to a predator, a declining probability of successful renesting) predict a reduced response through the nesting period. However, few studies have conclusively demonstrated behavioural habituation to repeated disturbance stimuli in birds (e.g., Siderius 1993; Walker et al. 2006), or shown that habituation can have a confounding effect on studies of the characteristics of nest defense (Mallory and Weatherhead 1993).

A further rationale for this study was to experimentally document how Great Blue Herons habituate. In contrast to the studies of nest defense behaviour outlined above, the generally more management-oriented investigations of breeding birds (e.g., Keller 1989; Lord et al. 2001), and especially Great Blue Herons (e.g., Vos et al. 1985; Rodgers and Smith 1995; Carlson and McLean 1996; Butler 1997), frequently have assumed that birds habituate to repeated nonthreatening human disturbances. But the potential interplay between the stage of the nesting period and habituation was not addressed properly in these studies. For example, none of the above studies used methodology to control for a revisitation effect or defined parental "investment" in terms of expected future opportunities (Montgomerie and Weatherhead 1988). In addition, previous studies have not used methodology that allows the pattern of habituation to be determined within and between nesting periods. Understanding the interplay between the influence of effects from the stage of the nesting period and those of behavioural flexibility will help to better understand the effects of disturbance on the productivity and distribution of Great Blue Herons and other nesting birds.

Materials and methods

Study area and colony sites

The study was conducted during 1998 and 1999 at 10 Great Blue Heron nesting colonies in south-coastal British Columbia, Canada (Table 1). Colonies were included in the study if they were active through the nesting period (i.e., fledged ≥1 nestling), and if the edge of the colony could be approached from a distance by the investigator at a steady pace and in clear view of several active heron nests. All sites except colony 30 had a visibility range from the investigator to the colony edge of at least 100 m. Colony 30 had a steep access route and a visibility range of about 50 m. Colonies were situated in relatively intact and fragmented woodlands. Colony sizes ranged from 34 to 322 nesting pairs. Nest configuration in colonies was largely determined by the type of trees that nests were situated in and fell into two broad categories. Colonies situated in conifers or large deciduous trees (e.g., black cottonwood, *Populus balsamifera* ssp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw) had a relatively high concentration of nesting pairs compared with colonies in smaller deciduous trees (e.g., red alder, *Alnus rubra* Bong.).

Investigator approach

The approach of an investigator was used to identify changes in Great Blue Heron response to potential disturbances through and between nesting periods by recording wildlife response distances (after Taylor and Knight 2003). A "heron response distance" was defined as the distance of the investigator from the colony perimeter at which >1 heron vocalized, moved from a nest, or took flight during an investigator approach. Colonies were approached directly and at a constant rate of about 60 steps per min (Erwin 1989; Rodgers and Smith 1995). The same investigator wore a dark hat and yellow rain coat on each visit. Care was taken to ensure that the speed and noise during the investigator approach were similar among all colonies. Response distances were flagged and a measuring tape was used to measure the distance once herons had vacated the site.

Rodgers and Smith (1995) defined a "response" as the movement of a breeding bird away from a nest site. To minimize disturbance to nesting herons in this study, both vocalizations and movement from a nest site were considered responses. The difference between these response definitions is small because movement of herons usually followed shortly after vocalizations (within a few seconds). Silence and alertness were not considered when determining response distance because they have a minimal energy expenditure and risk to the parent and thus have no clear fitness cost (Magnhagen 1991; Stearns 1992). If herons allowed the investigator to penetrate the colony edge before responding,

Table 1. Responses of Great Blue Herons (*Ardea herodias*) to the approach of a pedestrian investigator through the nesting period at 10 colonies in south-coastal British Columbia in 1998 and 1999.

				Response distance							
				Change through nesting period					Level of tolerance (m)		
Colony no.	Year	Colony size	No. of approaches (n)	F	P	r^2	m	b	Mean	Overall mean*	SE
1	2	48	24	—	—	—	—	—	—	—	—
13	1	304	5	0.2	0.7	0.07	–0.12	14.8	5.0	6.2d	1.2
	2	322	20	19.6	0.0003	0.52	–0.41	33.1	7.4		
23	1	190	20	25.9	<0.0001	0.59	–0.52	51.7	21.7	14.9cd	6.8
	2	174	12	14.8	0.003	0.60	–0.33	25.1	8.1		
25	1	50	12	8.7	0.02	0.47	–0.66	60.9	22.5	22.5c	—
14	1	37	11	13.4	0.005	0.60	–0.49	43.7	18.2	26.7c	8.5
	2	34	11	20.1	0.002	0.69	–0.56	61.9	35.2		
26	1	108	11	12.0	0.007	0.57	–0.43	45.2	18.2	28.6c	10.4
	2	107	6	2.6	0.2	0.39	–0.26	44.5	38.9		
28	1	60	11	15.0	0.004	0.63	–0.60	80.8	33.2	27.9c	5.3
	2	39	10	44.5	0.0002	0.85	–0.42	39.3	22.6		
27	2	120	12	5.9	0.04	0.37	–0.29	53.0	43.6	43.6ab	—
29	1	65	3	42.8	0.1	0.98	–1.87	146.8	58.3	54.8ab	3.5
	2	67	7	37.0	0.002	0.88	–0.66	84.4	51.3		
16	2	114	7	0.3	0.6	0.06	–0.36	72.9	60.1	60.1a	—

Note: Data are presented for primary approach routes only (the delayed approaches at colonies 13 and 23 are not included here). Heron responses to the approach of the investigator were observed at all colonies except colony 1. Year 1 refers to 1998 and year 2 refers to 1999. Colony size refers to the number of initiated nests in the colony. Colony numbers are after Vennesland (2000).

*Letters refer to significantly different groups of means at $\alpha = 0.05$.

the response distance was reported as a negative distance, measured inwards from the colony edge. This method was used because the response of herons generally increased as the investigator moved towards the centre of the colony.

Investigator approaches were initiated between 23 February and 13 April, corresponding to 28 days before first incubation to 34 days after first incubation (mean = 16 days after incubation, SD = 20 days, $n = 9$). There was no significant relationship between the date of initiation of the investigator approach relative to incubation and mean response distance ($P > 0.90$) or first response distance ($P > 0.80$). Variation in the initiation date of approaches between colonies and the duration of observations was due to differences in the phenology of colonies, access problems from fencing and flooding, and a delayed initiation of approach at one site owing to a local land manager. The duration of observations within a nesting period ranged from 50 to 128 days (mean = 83 days, SD = 28 days, $n = 15$).

For the controlled experiment to test for behavioural flexibility, two large colonies were used (>150 nesting pairs, $n = 2$). Two treatments of investigator approaches were used at each colony (i.e., a total of four separate approach routes at two colonies). This experiment was limited to these two colonies because only they were large enough to provide independent samples of herons to use in the different treatments. At each colony, the two treatments were situated on different sides of the colonies and were separated by at least 50 m throughout the nesting period. Both colonies were in woodlands composed primarily of red alder, with at most a few nests in each tree. Both colonies were >100 m in diameter at the narrowest divide. Herons in the different treatments were never visible to each other through the canopy and only a minimal response was elicited from only a few herons on each approach. Thus, herons in the different treatments were stimulated independently of each other. The "control" for the experiment consisted of delaying the initiation of the second investigator approach treatment from the incubation period until the nestling period (i.e., after hatching). This methodology allowed an examination of whether changes in heron response through the nesting period at these two colonies were due to the stage of the nesting period or flexibility in heron response to the disturbance stimulus.

In reference to the experiment, "primary approach" refers to the investigator approach treatment that occurred from incubation through the nestling stage, while "delayed approach" refers to the investigator approach treatment that occurred only through the nestling stage. Initiation of the two delayed approaches was deferred until 2 weeks after the first hatching event at each colony to ensure that most herons were rearing chicks and were no longer incubating. Heron nestlings are vocal and can be readily heard minutes after hatching (Butler 1997). Consequently, hatching was assumed if nestlings were seen or heard in a nest. The nesting stage of responding herons was similar for both treatments at each colony because they were nesting at the same colony. This experimental portion of the study was conducted only during the 1999 breeding cycle.

Predictions for the controlled experiment to test for behavioural flexibility were as follows. The expectation was that herons would reduce their response to the investigator approach through the nesting period, decreasing their response to (or increasing their tolerance of) the apparently benign disturbance stimulus through the nesting period because of either habituation to the stimulus or the stage of the nesting period. Tolerance was defined as the mean heron response at a nesting colony. Habituation was defined as an increase in tolerance (or reduction in response) through time not attributable to effects from the stage of the nesting period. Behavioural flexibility was defined as either an increase or a decrease in response through time not attributable to effects from stage of the nesting period. If herons adjusted their response simply because of the stage of the nesting period, the responses received on the delayed approaches should not have differed significantly from those on the primary approaches (i.e., lower overall mean, owing to the delay in approach initiation, and similar slope). Conversely, if herons adjusted their responses based on habituation alone, responses on the delayed approaches should have been significantly higher than, but with a similar slope to, those on the primary approaches (i.e., higher overall mean and similar slope). Finally, if herons adjusted their response owing to both the stage of the nesting period and habituation, the responses on the delayed approaches should have started significantly higher but converged with the primary approaches near the end of the nesting period (i.e., higher mean at outset of delayed approach, but similar overall mean, and higher slope).

Data analyses

Statistical analyses were conducted using Statistica (Statsoft Inc. 1999) and SAS (SAS Institute Inc. 1990). Because nesting phenology at colonies varied across the study area, all response dates for intercolony comparisons were adjusted with respect to the timing of nesting at each colony. First incubation (date of the first incubation of eggs by ≥1 heron) was defined as day zero for each colony. The onset of incubation was generally synchronous for most nests within colonies, so the first incubation event was a reasonable estimate of colony timing relative to the nesting period. Incubation was identified by the behaviour of herons on the nest — a heron was assumed to be incubating if it was observed lying flat on the nest early in the nesting period. Once incubation was confirmed with two consecutive visits to a nest, the first observation of a heron lying flat was used as day zero of incubation. The date of first incubation at colonies ranged from 12 March to 3 April (median 24 March, $n = 10$). In this study, mean response distance refers to the mean of all individual responses to investigator approaches at one colony in one nesting period (i.e., in 1 year). Overall mean response distance refers to the grand mean of the two mean response distances (at colonies with approaches in both years of the study). For colonies with observations in only 1 year, mean response distance equals overall mean response distance. First response distance refers to the response distance on the first investigator approach during a nesting period. Date of approach initiation refers to the date at which an investigator approach was begun at a colony.

The relationship between distance and date was tested using a repeated-measures ANCOVA assuming an autoregressive lag 1 (AR(1)) correlation structure between the repeated measurements for each colony year (SAS Institute Inc. 1990). Response distance was included in the model as the dependent variable (Y) and date relative to incubation was included as the independent variable (X). Colony and year and appropriate interactions with date were considered covariates. Significant interactions were identified between date and colony and colony and year ($P < 0.01$), so univariate regressions of heron response were conducted for each colony in each year (see Table 1). Differences in the overall mean response distances at individual colonies were tested using a Newman–Keuls test. Colony 1 was excluded from these analyses because no response was ever observed from herons at this site.

Univariate regressions were used to examine the relationships between mean response distance and colony size, mean response distance and date of approach initiation, and first response distance and date of approach initiation. A Student's t test was employed to determine if the mean response distance at colonies was related to the mean proportion of nests at colonies that failed to fledge any nestlings or to the relative number of nesting herons near the colony edge. For the latter analysis, colonies were grouped into two categories, those with a relatively high number of herons near the edge of the colony (≥10 nests; colonies 1, 14, 16, and 27) and those with a relatively low number of herons near the edge of the colony (<10 nests; colonies 13, 23, 25, 26, 28, and 29).

For the experiment to investigate whether changes in heron response through the nesting period at colonies 13 and 23 were due to the stage of the nesting period or the behavioural flexibility of herons, analyses centred on identifying differences in the mean response and differences in the slope of response between the primary and delayed approaches (see previous for an outline of experimental predictions). These analyses contained data only from 1999 because there were no delayed approaches used in 1998. To test for differences in the mean response between treatments, Student's t tests were used to determine if heron response was different on the primary and delayed approaches at both colonies. To examine whether there was a higher response at the outset of the delayed approaches compared with the same time period on the primary approaches, Student's t tests were conducted using only the first three responses on the delayed approaches and the three corresponding responses on the primary approaches (i.e., observations on the same dates). To test for differences in the slope of heron response between treatments, an ANCOVA was used to determine if the pattern of response was different on primary and delayed approaches. Significant interactions were identified between treatments at both colonies ($P < 0.05$), so four univariate regressions were performed on the responses of herons on each investigator approach at each colony.

Results

Changes in heron response with date

Changes in heron response to the approach of the investigator through the nesting period at 10 south-coastal British Columbia heron colonies are summarized in Table 1. Significant interactions were identified in the pattern of responses among colonies ($P < 0.01$) and between years ($P < 0.01$). Pooling observations and accounting for repeated observations over time at different colonies and over both years, herons significantly reduced their response distance through the nesting period by a mean of 0.48 m per day ($F_{[1,52.2]} = 74.66$, $n = 158$ observations, $n = 9$ colonies, $P < 0.0001$).

The same analysis determined that heron response was significantly higher in 1999 than in 1998 by a mean of 7.57 m (SE = 3.08 m) across all nine colonies where a response was observed ($t = 2.5$, $P < 0.05$). At colonies 13 and 23, negative distances were recorded late in the nesting period when herons would allow access beyond the colony edge before responding.

Colony differences in heron response

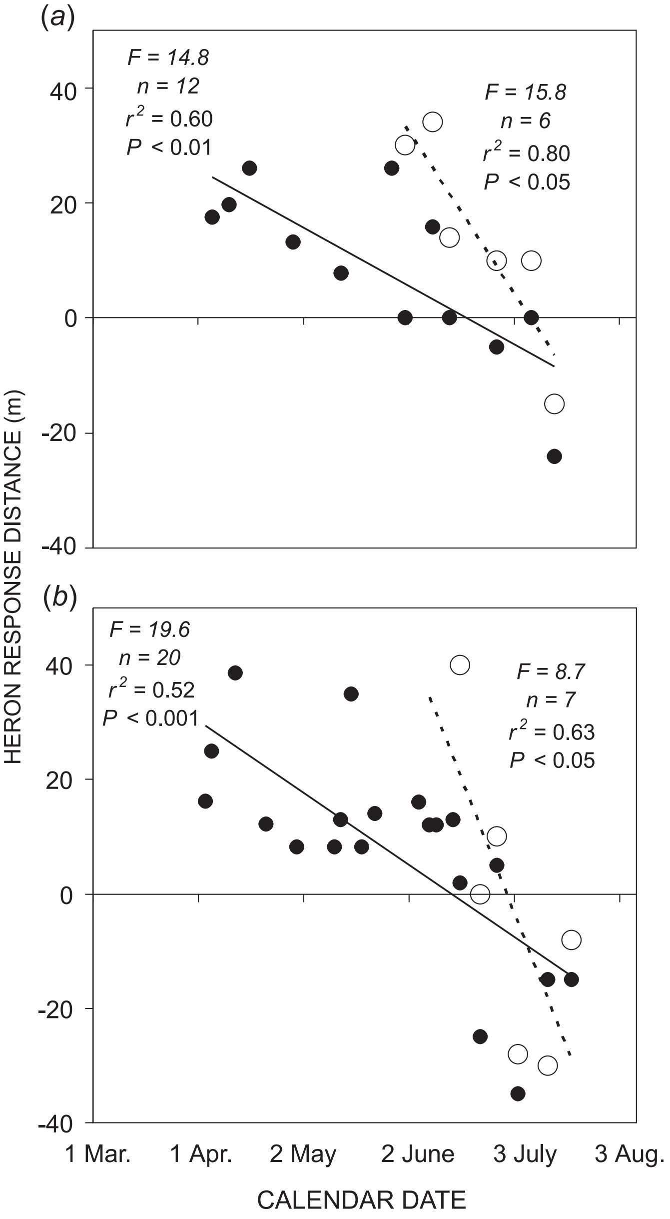
The pattern of change in heron response through the nesting period varied among colonies in south-coastal British Columbia (Table 1). The 15 regression slopes of heron responses from the nine colonies with observed responses varied in significance, although all slopes were negative and 11 of 15 slopes were significant at $\alpha = 0.05$ (except for colony 13 in 1998, colony 16 in 1999, colony 26 in 1999, and colony 29 in 1998; full statistics are listed in Table 1). The overall mean response distance from all colonies where a response was observed in 1998 and 1999 was 31.7 m (SE = 6.0 m, $n = 9$ colonies). Overall mean colony response distances fell into five significantly different but overlapping groups (Table 1). Colony 13 had the lowest observed mean response distance (6.2 m), and this mean was significantly different from the mean responses at all colonies except colony 23 (14.9 m). The highest mean response distance occurred at colony 16 (60.1 m), and the mean response at this colony was not significantly different from the mean response at colony 29 (54.8 m) or colony 27 (43.6 m). The maximum response distance observed at heron colonies varied from 35 to 100 m (mean = 74.2 m, SD = 25.0 m, $n = 9$). Minimum response distance ranged from –35 to 15 m (mean = –2.2 m, SD = 18.2 m, $n = 9$). There was no significant relationship between colony size (number of nesting pairs) and heron response distance at nine colonies where a response was observed ($P > 0.15$). There was no significant relationship between the mean proportion of nests that failed at colonies and the mean response distance ($P > 0.40$). There also was no significant relationship between the mean response distance at colonies with a relatively large number of nests near the edge of the colony ($n = 4$) and those with a relatively small number of nests near the edge of the colony ($n = 6$; $P > 0.30$).

Changes in heron response controlling for date

For the experimental treatments, mean heron response on the delayed approaches was not significantly different than on the primary approaches at both colony 13 ($t = 0.74$, $P > 0.20$; Fig. 1*a*) and colony 23 ($t = -0.43$, $P > 0.30$; Fig. 1*b*). However, mean heron response at the outset of the delayed approaches (first three observations only) was significantly higher than the mean response on the three corresponding observations of the primary approaches at both colony 13 ($t = 4.34$, $P < 0.05$; Fig. 1*a*) and colony 23 ($t = 7.42$, $P < 0.01$; Fig. 1*b*).

Testing the slopes between primary and delayed approaches, the interaction between date and treatment group was significant for heron responses at both colony 13 ($P < 0.05$) and colony 23 ($P < 0.01$). The slopes of heron responses through the nesting period therefore differed significantly between primary and delayed approaches at both colonies. Univariate regressions of heron response distance versus date relative to incubation declined significantly through the nesting period for both primary and delayed approaches at both colony 13 (primary approach: $F_{[1,22]} = 14.8$, $n = 12$, $r^2 = 0.60$, $P < 0.01$; delayed approach: $F_{[1,10]} = 15.8$, $n = 6$, $r^2 = 0.80$, $P < 0.05$; Fig. 1*a*) and colony 23 (primary approach: $F_{[1,38]} = 19.6$, $n = 20$, $r^2 = 0.52$, $P < 0.001$; delayed approach: $F_{[1,12]} = 8.7$, $n = 7$, $r^2 = 0.63$, $P < 0.05$; Fig. 1*b*).

Fig. 1. Results from the date controlled investigator approach experiment conducted in 1999 at (*a*) colony 13 and (*b*) colony 23. Solid data points refer to heron response distances on primary approach routes (●), whereas open data points refer to response distances on delayed approach routes (○). Significant interactions between treatment groups were identified at both colonies ($P < 0.05$).



Discussion

Great Blue Herons nesting in south-coastal British Columbia reduced their behavioural response to repeated and ultimately nonthreatening human activity through the nesting period, and increased their response in the second year of the study. It was experimentally demonstrated that nesting Great Blue Herons, presented with a novel disturbance stimulus from humans part way through the nesting period, adjusted their response through the remainder of the nesting period to eventually converge with an independent group of herons at the same colony and exposed to the same activity since the start of the nesting period. That is, Great Blue Herons habituated to the disturbance stimulus, but also responded based on the stage of the nesting period. This study therefore provides experimental evidence for the potential of habituation to methodologically confound conclusions about the characteristics of avian nest defense behaviour, and demonstrates that Great Blue Herons can habituate behaviourally to the approach of a pedestrian within a nesting period.

Changes in heron response with date

Heron response declined through the nesting period to the repeated and standardized approach of an investigator. A significant decrease in the response distance of herons was observed for all data pooled and for 11 of 15 separate investigator approaches over both years of the study at the nine colonies where a response was observed. Of the four regressions that were not significant, three had the fewest number of approaches (i.e., lowest sample sizes) in the study, likely accounting for the lack of significance on these approaches and the overall significant interaction of colony by date. Based on this, the colony by date interaction likely has no biological significance. The lack of response from herons at colony 1 presumably was due to the frequent human presence below and around the colony. This colony is situated in an urban park in the city of Victoria and has near-continuous human activity directly below the nests, including vehicles and pedestrians.

Herons responded more strongly to the disturbance stimulus in 1999 than in 1998. It is not clear if this was due to an amplified response from parental experience (e.g., as per Forbes et al. 1994), or an artifact of sampling only 2 years. A longer study controlling for date would be required to differentiate between these hypotheses.

Colony differences in heron response

The colonies in this study showed significantly different levels of tolerance to the risk presented to herons by the investigator approach. Because the effect from the stage of the nesting period should be equivalent across all colonies and given the experimental results of this study, this variation likely is due largely to prior habituation to human activity in this relatively developed (Boyle et al. 1997) region. This is illustrated by a comparison of the mean response distances from this study to an index of human development produced for this region by Vennesland and Butler (2004). Comparison of overall mean response distances to this human development index (with three classes of urbanization — urban, suburban, and rural) showed a significant and positive correlation ($F_{[1,16]} = 6.0$, $n = 9$, $P < 0.05$). With the widespread, variable, and frequent human activity that occurs in this region, habituation likely has occurred to the past presence of humans. Other authors also have suggested that differences in avian tolerance levels to human disturbance represent the result of habituation (Vos et al. 1985; Keller 1989; Carlson and McLean 1996; Butler 1997; Lord et al. 2001), but it is problematic to conclusively determine this without experimentation (see next section).

Gill et al. (2001) point out that avoidance of disturbance also could be affected by the availability or quality of other nesting locations in the area compared with the site that is occupied. Herons commonly move between sites in this region (Simpson et al. 1987), so the availability of other sites should not be a limiting factor for nesting herons. However, the quality of sites may be variable, both in terms of food availability or pollution (Butler 1997; Elliott et al. 2005) and of disturbance (Vennesland and Butler 2004).

Changes in heron response controlling for date

Herons in this study reduced their response through the nesting period, implying that they habituated to the repeated stimulus owing to a reduced perception of risk. However, other phenomena determined by the stage of the nesting period, such as the potential for renesting or the value of the brood to a predator, also would predict a decrease in response through the nesting period (Knight and Temple 1986; Montgomerie and Weatherhead 1988). The effect of date therefore must be controlled to properly establish if an observed behaviour is determined by parental experience with a stimulus (e.g., habituation) or the stage of the nesting period.

The results of the experiment controlling for the effect of date indicate that herons responded flexibly and habituated to the investigator approach, although factors based on the stage of the nesting period also had influence. Heron responses on the delayed approaches began at a similar level to those on the primary approaches even though the initiation of the delayed approaches was deferred until the nestling period. Heron response on the primary and delayed approaches then converged near the end of the nesting period. Furthermore, the decrease in response was significant on primary and delayed approaches at both colonies, responses on both of the delayed approaches decreased at a significantly faster rate than on the primary approaches, overall mean response was not significantly different between primary and delayed approaches, and the mean response was significantly higher at the outset of the delayed approaches than over the same time period on the primary approaches. Thus, herons at these colonies exhibited flexibility towards repeated nonthreatening human intrusions into nesting colonies and reduced their response through the nesting period (i.e., they habituated), but also responded based on the stage of the nesting period. It is important that behavioural flexibility is accounted for in studies using the repeated disturbance of animals (Montgomerie and Weatherhead 1988) to ensure a proper assessment of observed patterns in behaviour.

Montgomerie and Weatherhead (1988) reviewed specific factors that are determined by the stage of the nesting period that might affect avian response to disturbance stimuli. Of the factors Montgomerie and Weatherhead (1988) described, the following have the potential to have influenced heron response in this study: increasing nest conspicuousness, an increase in the value of the brood to the predator, a declining potential for renesting for the parents, and (or) a decreasing difference between the survival probabilities of the parent and the offspring. Increasing nest conspicuousness through the nesting period is unlikely to have influenced heron response because heron nests are usually located near the top of trees and colonies are obvious (Butler 1997). The expected increase in the value of the nest contents to predators did not appear to be important because predators frequently prey on eggs, as well as nestlings (Butler 1997; Vennesland and Butler 2004), and in 1999 a similar number of eagle attacks were witnessed during both the incubation and nestling periods at 31 colonies (unpublished data). The potential for renesting might have had a notable influence on heron response because the ~170 day nesting window for herons in this region (Vennesland 2000) is much longer than the 100 days they require (Butler 1992, 1997), providing ample time to attempt nesting more than once. Vennesland (2000) documented a frequent reuse of nests in 1999 (25% of 208 nests, at 77% of 17 colonies), though it was unclear whether the reuse was by the same or different nesting pairs. Furthermore, colony abandonment is most common early in the nesting period (Vennesland and Butler 2004). The survival probability of nestlings also might have influenced heron response through the nesting period. The relative difference between the expected future survival of the offspring and that of the parent declines with increasing offspring age (Andersson et al. 1980), so the relative importance of the expected reproductive productivity of the offspring for the fitness of the parent should increase through the nesting period.

Management implications

This study demonstrated that Great Blue Herons habituated behaviourally to a low-level human disturbance stimulus. Although this may bode well for the ability of herons to persist in areas with low-level human use, this result should be used with caution in heron management for several reasons.

The decision of how to respond to a potential disturbance stimulus is to some degree inflexible for Great Blue Herons because it depends on factors determined by the stage of the nesting period. Thus, irrespective of the influence of habituation, the presence of a significant effect from the stage of the nesting period means that caution must be exercised with regard to disturbing heron colonies, especially early in the nesting period when experience with a stimulus is limited. Several other studies have recommended similar caution about the timing of disturbance for Great Blue Herons and other species of waterbirds (reviewed by Parnell et al. 1988; Carney and Sydeman 1999).

It additionally should be noted that the stimulus used in this study was of a very low level. The results presented here therefore cannot be used to predict heron response to larger disturbances associated with human activity (groups of people, pets, loud voices, machinery, etc.) at any time of the season. As with the timing of disturbance events, several previous studies have recommended caution with regard to the magnitude of stimuli (reviewed by Parnell et al. 1988; Carney and Sydeman 1999).

Furthermore, human-dominated habitats may not represent a high-quality environment, even if birds are habituated to a benign human activity within them. Other studies have demonstrated that birds nesting in areas with high levels of human activity that were apparently habituated had lower nesting success than birds nesting in areas with lower levels of human activity (e.g., Keller 1989; Lord et al. 2001; Skagen et al. 2001; Vennesland and Butler 2004). Similarly, studies of birds have shown that human presence can negatively affect foraging behaviour (e.g., Ward and Low 1997; Ronconi and St. Clair 2002). Possible explanations for reductions in habitat quality for nesting Great Blue Herons in British Columbia include habitat availability (Butler 1997), human and predator disturbance (Vennesland and Butler 2004), and industrial pollution (Elliott et al. 2005). In addition, disturbance from predators or humans also may negatively affect nesting birds through a stress response from increased corticosterone levels (Walker et al. 2006).

The stronger heron response observed at nesting colonies in 1999 compared with 1998 suggests that the influence of the stage of the nesting period might have overwhelmed the behavioural flexibility of herons between the 2 years of the study (similar to that reported for Northern Mockingbirds, *Mimus polyglottos* (L., 1758), by Breitwisch 1988). Stable habituation that holds between years thus may be a longer term process than this study was able to document. It also is possible that habituation occurs on an annual basis. Great Blue Herons in this region move frequently between colonies between years (Simpson et al. 1987), yet the response level at specific colonies in this study remained relatively stable between years. Thus, individual herons that change sites between years may assess the appropriate level of response based on the behaviour of other individuals at the site they are currently nesting at, not on their experience with disturbance stimuli from previous years at other sites.

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