Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls

Ryan J. Fisher, Ray G. Poulin, L. Danielle Todd, and R.M. Brigham

Abstract: The effect of nest stage on nest defence responses has been fairly well established but the impact of weather conditions has been largely ignored. We examined the effects of nest stage, number of previous visits, wind speed, and air temperature on burrowing owl (Athene cunicularia (Molina, 1782)) defence of nests from a human intruder. We found that burrowing owls changed nest defence tactics from retreat behaviour to more confrontational behaviour once eggs hatched. Aggressiveness was significantly reduced as wind velocity increased and when temperatures were warmer. We found no evidence for a change in owl defence behaviour with the number of previous visits to a nest. Although not statistically significant, there was a tendency for burrowing owls to allow closer approaches and to not retreat as far once eggs had hatched. Wind speed did not have an effect on retreat or approach distances, and owls allowed us to get significantly closer to the nest before retreating when air temperatures were warm. There are a multitude of factors that could affect nesting success and thus fitness of birds, but our study shows that routine climatic events such as warm weather had a measurable impact on how a bird defended its reproductive investment.

Résumé : Les effets du stade de nidification sur les réactions de défense du nid sont bien connus, mais, l’impact des conditions météorologiques sur la défense a été peu étudié. Nous avons examiné les effets du stade de nidification, du nombre de visites antérieures, de la vitesse du vent et de la température sur le comportement de défense du nid chez la chevêche des terriers (Athene cunicularia (Molina, 1782)) contre un intrus humain. Une fois les œufs éclos, les chevêches modifient leurs tactiques de défense, d’un comportement de fuite à un comportement plus belliqueux. L’agressivité décroit significativement aux vitesses de vent plus fortes et aux températures plus chaudes. Il n’y a pas d’indication d’un changement de comportement de défense chez la chevêche en fonction du nombre de visites antérieures au nid. Bien que non statistiquement significative, il y a une tendance chez les chevêches à laisser les intrus s’approcher plus et à ne pas fuir aussi loin une fois que les œufs sont éclos. La vitesse du vent est sans effet sur la fuite ou la distance d’approche tolérée; aux températures de l’air plus élevées, les chevêches nous ont laissé nous approcher significativement plus près du nid avant de prendre la fuite. Il y a une multitude de facteurs qui peuvent potentiellement affecter le succès de la nidification et donc le fitness des oiseaux, mais notre étude fait ressortir comment des événements climatiques communs, comme par exemple, du temps chaud, ont un impact mesurable sur le comportement d’un oiseau pour défendre son investissement reproductif.

Introduction

Protecting reproductive investment has obvious fitness consequences. Constructing a well-concealed or inaccessible nest and exhibiting active defence behaviours are two ways that birds can protect their offspring (Cresswell 1997). Nest defence has typically been assessed by measuring the distance an intruder is allowed to approach before the parent bird leaves the nest and the level of aggression parent birds use in confronting an intruder (see Montgomerie and Weatherhead 1988 for a review).

The decision about when to retreat from the nest requires parent birds to balance the likelihood of an inevitable retreat against that of an unnecessary retreat. If an intruder is inevitably going to force the bird to leave its nest, the parent bird should vacate early to minimize the risk to itself and the risk of revealing the nest location (Andersson et al. 1980). If the intruder is inevitably going to bypass the nest, then parent birds should stay on the nest, conserving their own energy and continuing thermoregulatory duties. Ultimately, the decision of when to retreat is affected by factors such as accessibility of the nest (Montgomerie and Weatherhead 1988), predator type (Lima and Dill 1990), longevity of adults (Hatch 1997), and the amount of energy already invested in the offspring (Andersson et al. 1980).

Once a bird has vacated its nest, it must then decide whether or not to actively defend the nest. Because of their relative speed, agility, and aerial advantages, most avian species are well suited to engage terrestrial predators with minimal risk to themselves. Some species resort to “broken
wing displays intended to distract intruders and thus prevent them from finding the nest (Gramza 1967; Barash 1975); others are known to swoop and harass intruders at the nest, while raptors can defend even more vigorously by inflicting injury to would-be nest predators (Montgomerie and Weatherhead 1988; Carrillo and Aparicio 2001).

An important factor affecting the type of defence behaviour employed by parent birds is their future reproductive potential and that of their offspring. The “reproductive value” hypothesis suggests that nest defence strategies of altricial species should intensify as their offspring progress through stages of the nesting cycle (Andersson et al. 1980). As young get older, there is a greater likelihood that they will fledge; thus they become increasingly more valuable to the fitness of their parents (Rytkonen et al. 1995; Olendorf and Robinson 2000; Pavel and Bureš 2001; Gunness and Weatherhead 2002; see Montgomerie and Weatherhead 1988 for a review). Since the reproductive value hypothesis was proposed, most studies have considered offspring age when assessing nest defence behaviours; however, few have tested the potential effects of weather conditions (Gunness and Weatherhead 2002). Most studies have simply controlled for weather conditions by testing defence behaviour only on days with favourable environmental conditions (Andersen 1990; Sproat and Ritchison 1993). When ambient temperatures are outside the thermal neutral zone, birds face additional energy costs that could affect their decisions on nest defence strategy. Furthermore, behaviour of adult birds can also be influenced indirectly through weather effects on their nestlings (i.e., harm to offspring hypothesis, Bureš and Pavel 1997). It seems logical that wind conditions may also adversely affect nest defence behaviours; however, this hypothesis has never been explicitly tested. The percentage of eggs lost at thick-billed murre (Uria lomvia (L., 1758)) nest sites under windy conditions was almost twice that taken under calm conditions (Gilchrist and Gaston 1997). However, this difference was attributed to predator advantages under windy conditions and not reduced defence capabilities of the guarding parents (Gilchrist and Gaston 1997). Interestingly, these weather factors have been largely ignored when assessing nest defence behaviours.

The purpose of our study was to determine how nest stage and weather conditions affect the nest defence behaviours of burrowing owls (Athene cunicularia (Molina, 1782)), small (≈150 g) birds of prey inhabiting the grasslands and arid regions of western North America. Burrowing owls nest in the abandoned burrows of animals such as prairie dogs (Cynomys ludovicianus (Ord, 1815)), ground squirrels (Spermophilus spp.), and badgers (Taxidea taxus (Schreber, 1777)) and are capable of escaping avian predators by retreating underground. However, nesting underground makes owl nests susceptible to fossorial predators such as badgers, foxes (Vulpes vulpes (L., 1758)), and weasels (Mustela spp.; Haug et al. 1993; Todd et al. 2003).

We tested whether individual male burrowing owls’ nest defence behaviours change with nest stage, predicting that defence should intensify with nest age if the reproductive value hypothesis is true. We also tested whether burrowing owl nest defence behaviour changes with weather conditions (wind and temperature). Specifically, we predicted that inclement weather would likely increase costs associated with nest defence, either through increased energetic demands (i.e., extreme heat) or increased risk due to flight difficulties (i.e., wind), and thus decrease apparent parental aggressiveness.

Materials and methods

From May through July 2002, we studied burrowing owls on the Regina Plain in southern Saskatchewan, Canada. The study area encompassed 12 200 km² between the cities of Moose Jaw (50°34′N, 105°17′W), Regina (50°25′N, 104°39′W), and Weyburn (49°40′N, 103°52′W). The habitat in this area was historically moist-mixed grassland but is now dominated by the production of cereal crops (Gauthier et al. 2002). Burrowing owls in this area nest in burrows excavated by Richardson’s ground squirrels (Spermophilus richardsonii (Sabine, 1822)) and badgers, and in nest boxes. The nest boxes allowed us to gather precise data on nest stage and should have had no effect on the defence behaviour of the owls (but see Sproat and Ritchison 1993). Nest boxes were placed at approximately the same depth under the ground as natural burrows, were buried with soil, which provided insulation, and had open floors, which provided natural soil and moisture conditions. Therefore, we are confident that owls using either natural burrows or nest boxes experienced similar microclimatic conditions. During the course of our study, owls had little or no contact with humans other than us.

Clutch initiation occurred throughout May. During incubation, females remained inside the burrow most of the time while males roosted outside the nest or on a perch close to the nest. Hatching occurred from early June until early July; during this period, females began to spend increasingly more time outside of the nest burrow. Owlets began to emerge from their burrows as early as 10 to 15 days post hatch and young fledged at approximately 41 days post hatch (Todd 2001).

We measured clutch size, hatch date, nest stage, and nest success at nests in 13 boxes. Nest stage of nests in natural burrows (N = 11) was estimated based on female sightings and behaviours. If a female was not observed above ground, we assumed that she was incubating eggs (Haug et al. 1993). If a female was seen outside of the burrow for prolonged periods, we assumed that the nest was at the posthatch stage. Males and females at our study sites were captured and banded with sex-specific colour bands to make identification easier. For those nests where banded owls were not present, males were distinguished from females by their lighter plumage coloration (Martin 1973). Because females were rarely present outside the burrow, analysis of female nest defence was not possible; therefore, all the results we present are for male nest defence behaviour only.

We assessed nest defence behaviour at each nest every third day; however, other visits to the nests were made over 2 months to collect data for other studies (mean (±SD) number of visits per nest = 15.8 ± 9.1). Except for data pertaining to the number of nest visits, extraneous visits are not included in this paper. Nest visits always occurred between 0830 and 1700. The observer approached the nest from a direction where the owl had an unobstructed view of the approach. To keep trials consistent, the same observer ap-
proached all nests with an upright posture and at a medium pace (see Knight and Temple 1986a). Once an owl flew from the nest, we measured the distance between the observer and the owl at the time of retreat (approach distance) and the distance the owl landed from the nest (retreat distance) using a Bushnell digital rangefinder (+1 m). Once the owl had landed, the observer kept walking along a straight line to the nest. With a compass we measured the direction of the observer’s approach and the direction in which the owl flew, as well as the direction of the sun relative to the nest. We calculated the mean difference between approach and retreat directions (maximum difference of 180°) to determine retreat paths of owls. At nests in nest boxes, we recorded clutch size, nest stage, and the number of young at each visit. To maintain consistency in the length of time we spent at each nest, approximately 3 to 5 min were spent at natural nests to simulate the time it took to conduct a nest box check.

To maintain consistency of wind speed measurements across trials, one observer (R.J.F.) classified wind speed as light (0 to 20 km/h), medium (20 to 40 km/h), or high (>40 km/h) and recorded ambient temperature at the beginning of each trial. To attain the greatest possible paired sample sizes, we classified temperatures into two groups, 12–22 °C and 23–31 °C.

We ranked behavioural responses from zero (no nest defence) to five (a maximum level of defence) to assess male nest defence (Table 1). We used this ranking system as a measure of the aggressiveness of the defence response: scores of 2 or less indicated that the observer’s approach elicited no defence response, whereas scores equal to or greater than 3 indicated that the approach elicited increasingly aggressive defence behaviours and thus represented increased risk to the bird.

All statistical tests were two-tailed analyses. Because defence behaviour was a ranked variable, we used repeated measures or paired nonparametric statistical tests to assess the effects of nest stage, number of previous visits, air temperature, and wind speed on nest defence behaviour. We used repeated measures or paired parametric tests to analyze the effects of nest stage, number of previous visits, air temperature, and wind speed on approach and retreat distances. Because we used separate analyses (using different combinations of nests) for wind speed and temperature effects, we were not able to assess whether there was an interaction between the two variables. Specific tests are noted in the Results. Variables were grouped into three nest stages for analysis: prehatch (1–3 days before hatch), first week post hatch (1–7 days after hatch), and third week post hatch (14–19 days after hatch). This allowed us to conduct more powerful analyses (i.e., repeated measures) by tracking the behavioural changes of individuals over time. For those nests in natural burrows, hatch date was approximated and ranges may therefore be slightly wider than reported; however, we are confident that our estimate of hatch date was accurate to ±5 days.

**Results**

**Defence behaviour**

Owls flushed in a mean (±SE) direction of 116° ± 3° (N = 161) from our approach, where 180° would be flying directly away from us, 90° perpendicular to us, and 0° directly towards us. Owls tended to fly perpendicular to the direction of the sun (84° ± 12° (mean ± SE), N = 24). Individuals significantly increased the intensity of their nest defence behaviour from the prehatch stage to the first week post hatch and then remained at this higher level in the third week post hatch (Friedman nonparametric repeated measures ANOVA; χ² = 9.53, p < 0.01, N = 16; Fig. 1). Specifically, nest defence scores were significantly higher in the first week post hatch (multiple comparison critical difference test; rank difference = 13.5, number of comparisons = 3, p = 0.05) and the third week post hatch (rank difference = 13.5, number of comparisons = 3, p = 0.05) than at the prehatch stage. Since average nest defence was most intense in the first week post hatch, we used behaviours recorded during this period to determine the effects of weather and number of previous visits on behaviour, thereby controlling for nest stage. Individuals significantly decreased their aggressive behaviour with increasing wind speed (Friedman nonparametric repeated measures ANOVA; χ² = 10.94, p < 0.01, N = 9; Fig. 2). Birds had significantly lower defence scores at high wind speeds than at low wind speeds (multiple comparison critical difference test; rank difference = 11.5, number of comparisons = 3, p < 0.05). Aggressiveness also decreased at higher temperatures (Wilcoxon matched pairs test; z = 2.12, p < 0.05, N = 16; Fig. 2). The number of preceding visits to a nest was not significantly correlated with nest defence (Spearman rank correlation; r = 0.35, p = 0.14, N = 19).

**Approach and retreat distance**

There was no statistically significant change in the distance we were allowed to approach from the prehatch stage to the third week post hatch (repeated measures ANOVA; F = 1.72, p = 0.20, N = 14). However, 10 of the 14 owls tested allowed us to approach closer during the first week after hatch than before hatch. On average, we were able to approach to within 69 m (SE = 11 m) before hatch, 50 m

---

**Table 1. Ranked nest defence behavioural responses of burrowing owls (Athene cunicularia) to a human intruder.**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Description of owl behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Retreats into burrow</td>
</tr>
<tr>
<td>1</td>
<td>Flies, lands, does not return to nest, and performs no vocalizations</td>
</tr>
<tr>
<td>2</td>
<td>Flies, lands, and does not return to nest, but performs an alarm call (chatter)</td>
</tr>
<tr>
<td>3</td>
<td>Flies, lands, and returns to nest, but does not perform chatter</td>
</tr>
<tr>
<td>4</td>
<td>Flies, lands, returns to nest, chatters, and hovers overhead</td>
</tr>
<tr>
<td>5</td>
<td>Flies, lands, returns to nest, chatters, and dives at intruder</td>
</tr>
</tbody>
</table>

© 2004 NRC Canada
Burrowing owls flew an average of 120 m (SE = 13 m) from the nest in the prehatch period, 75 m (SE = 16 m) in the first week post hatch, and 80 m (SE = 19 m) in the third week post hatch (F = 3.08, p = 0.06, N = 14). There was no significant effect of wind speed on either approach or retreat distance in the first week post hatch (repeated measures ANOVA; approach distance, F = 2.30, p = 0.13, N = 9; landing distance, F = 0.591, p = 0.57, N = 9). Approach distance significantly decreased with increasing temperature during the first week post hatch (paired t test; t = 5.67, p = 0.03, N = 16; Fig. 3); however, retreat distance was not affected by temperature (paired t test; t = 1.14, p = 0.27, N = 16).

Discussion

Effects of nest stage

According to the reproductive value hypothesis, altricial species should increase the vigour of their nest defence with increasing offspring age (Andersson et al. 1980; Montgomerie and Weatherhead 1988). Many studies involving raptors such as merlins (Falco columbarius L., 1758; Wiklund 1990), red-tailed hawks (Buteo jamaicensis (J.F. Gmelin, 1788); Andersen 1990), eastern screech-owls (Otus asio (L., 1758); Sproat and Ritchison 1993), and Eurasian kestrels (Falco tinnunculus L., 1758; Carillo and Aparicio 2001) have reported results consistent with this hypothesis. In our study, burrowing owls displayed an increase in defensive intensity between prehatch and posthatch nesting periods (Fig. 1), switching from a retreat strategy during egg incubation to more confrontational behaviour after the eggs had hatched. This provides further support for the reproductive value hypothesis and suggests that for altricial species, a hatched egg has substantially more value than even a late incubation stage egg.

The distance an intruder can approach before eliciting a response has been used as a measure of nest defence for species whose actions could reveal the nest location to a potential predator (Rätti 2000; Gunness and Weatherhead 2002). While we did not find a statistical difference in the approach or retreat distances between pre- and posthatch nests, individual owls allowed us to approach an average of 19 m closer to the nest after the eggs had hatched and they retreated an average of 46 m farther before hatch. That is, owls were more likely to stay on their nest longer and did not retreat as far once eggs had hatched. If nest defence behaviour is correlated with nest stage, as predicted by the reproductive value hypothesis, our observations suggest that staying at the nest longer may be a means to keep the location of the nest hidden as long as possible (Weidinger 2002). Furthermore, not flying as far away might be a strategy to position the owl close enough to quickly confront an intruder if necessary.

There is debate as to whether animals become positively reinforced after successful nest defence in response to familiar human intruders (Knight and Temple 1986a, 1986b). We found that the number of previous visits had no significant effect on aggressiveness, approach distance, or retreat distance of burrowing owls. Nest visits were frequent enough (only one nest had fewer than 5 visits and most nests were visited more than 10 times) that habituation would have been controlled for in the analyses by being consistently high among all nests. There is also debate as to whether humans elicit natural nest defence responses in animals (Knight and Temple 1986a). Frid and Dill (2002) suggest that when animals encounter human disturbance they are likely to follow a cost–benefit analysis similar to that used by prey in predatory situations. We have no evidence to suggest that our intrusions induced unnatural nest defence, since

© 2004 NRC Canada
our observations were similar to those described by Martin (1973) for natural burrowing owl predators and similar to our observations of burrowing owls responding to coyotes (*Canis latrans* Say, 1823; R.G. Poulin, personal observations).

**Retreat direction and distance**

Burrowing owls in our study retreated in a direction roughly perpendicular (116° ± 3°) to our approach. By doing so, they would potentially lead intruders away from the nest in a manner similar to “broken wing” displays (Gramza 1967; Barash 1975). Owls exhibited no tendency to fly in the direction of the sun. We had speculated that flying in the direction of the sun would allow a retreating or defending owl to “vanish” from a predator’s field of vision. Anecdotally, we have regularly observed burrowing owls hovering and swooping at an observer from a position directly between the observer and the sun. By using the sun to blind intruders to their approach, burrowing owls could lessen the risk to themselves while defending the nest.

**Effects of weather**

Few studies have attempted to address the effects of weather on nest defence. Gunness and Weatherhead (2002) found that weather conditions had no appreciable effect on approach distance of three duck species, but in general, nest defence studies have attempted to standardize or control for weather conditions. We found that burrowing owls significantly altered their nest defence behaviour under differing weather conditions. Even when burrowing owl nest defence behaviour was highest (first week post hatch), we still observed a substantial reduction in nest defence (basically, retreating instead of defending) during windy or warm conditions.
When winds were light, burrowing owls aggressively defended their nest, whereas in windy conditions the owls tended to simply retreat. It is possible that under windy conditions, owls may have more difficulty hovering and accurately swooping at intruders; therefore, to minimize the risk to themselves, they simply retreat.

High ambient temperatures likely make defence behaviours energetically more costly for parent birds. Burrowing owls maintain constant body temperature between ambient temperatures of 0–38 °C (Coulombe 1968), but as ambient temperatures rise outside of their thermal neutral zone, birds must expend energy (e.g., gular flutter) to stay cool. We regularly observed burrowing owls using gular flutter at ambient temperatures approaching 30 °C on days when we conducted defence trials. For grassland species (such as burrowing owls), which typically do not have access to shade while guarding their nest, direct sunlight may compound effects of warm temperatures even further. We speculate that heat-stressed burrowing owls must reduce the vigour of their nest defence behaviour simply for energetic reasons.

We have shown that something as ubiquitous as acute weather phenomena can affect the nest defence of burrowing owls and presumably have a potential impact on parental fitness through reproductive success, energy expenditure, or predator exposure. This potential fitness consequence leaves questions about how an elongated period of inclement weather could affect population dynamics of an endangered species such as the burrowing owl.

Acknowledgments

We are grateful to Wildlife Preservation Trust Canada, World Wildlife Fund Canada and Environment Canada (Endangered Species Recovery Fund), Natural Sciences and Engineering Research Council of Canada, and Saskatchewan Environment for significant contributions to all burrowing owl work that we have undertaken in Saskatchewan. We appreciate the tremendous support of G.L. Holroyd, T.I. Wellicome, W. Harris, and all members of the Canadian Burrowing Owl Recovery Team. We offer special thanks to those landowners who believe in and practice management activities that consider the best interests of burrowing owls and the badgers, ground squirrels, and prairie dogs that they depend on.

References


Rätti, O. 2000. Characteristics and level of aggression by female Pied Flycatchers at different distances from the nest hole. Ornis Fenn. 77: 11–16.