The effects of heat stress, predation risk and parental investment on Malaysian plover nest return times following a human disturbance

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ABSTRACT

Waders leave nests and conduct distractive displays when approached by people. The time taken for waders to return to nests depends on numerous factors that affect the costs and benefits of incubation and anti-predator behavior. Understanding this trade-off may help assess the reproductive consequences of different nest return times and identify variables to consider in breeding disturbance studies. We subjected 73 Malaysian plover (*Charadrius peronii*) nests to standardized human disturbances and an analysis of covariance was used to determine how weather, time of day, embryonic age, weeks into breeding season and nest attendance (proportion of time adults incubated nests) influence nest return times. Egg temperatures were estimated using a regression model that predicted the temperature inside unshaded eggs from air temperature, cloud cover and time of day ($r^2 = 0.88$). We assessed the relationship between nest return times and hatch success. Plovers returned to nests faster at higher modeled egg temperature ($P = 0.010$), in the morning ($P = 0.003$), if they had younger clutches ($P = 0.038$), and if they had high nest attendance prior to the disturbance ($P = 0.015$). Pairs that returned to nests faster had lower hatch success ($P = 0.021$). This may be because pairs that spend more time distracting humans may also do so for predators. These results suggest that short nest return times may not indicate low fitness costs of disturbance. The thermal and predation environment in addition to nest return times should be taken into account when assessing the deleterious effects of human disturbance.

1. Introduction

An animal's response to a person depends on both the extent of the perceived threat as well as the possible fitness consequences of the response (Frid and Dill, 2002; Yasué, 2006). Although many researchers have examined how the perceived threats (e.g. people running versus walking) affect behavior (Lord et al., 1997; K. Thomas et al., 2003), few studies have assessed how costs to adult survivorship or productivity influence responses (Stillman and Goss-Custard, 2002; Beale

and Monaghan, 2004a) and even fewer have examined this in breeding birds (Beale and Monaghan, 2004b).

With more people visiting beaches, beach-nesting waders may be increasingly vulnerable to adverse impacts of human disturbance (Burger, 2000; Lord et al., 2001). A better understanding of the trade-offs that shape the response of breeding waders to human "predators", may elucidate the relationship between the observed behavioral responses of wildlife to people and reproductive costs (Gill et al., 2001). This may help managers identify locations, times or populations in which

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human disturbance may be most likely to affect wader survivorship or productivity (Weston and Elgar, 2005).

Temperature regulation of clutches by parental incubation or shading is a key factor affecting hatching success (Webb, 1987). However, when people approach small wader nests (*Charadriidae* and *Scolopacidae*), adults will often leave the nest and attempt to lead people away with conspicuous behaviors such as calling, feigning injury, "rat-running" or false-brooding (Gochfeld, 1984). Eventually the parent will return to the nest discreetly to avoid leading a predator to the nest (Weathers and Sullivan, 1981). This study examines factors influencing the time taken for a ground-nesting tropical wader, the Malaysian plover (*Charadrius peronii*), to return to a nest after a standardized human disturbance ("nest return times").

Nest return times are influenced by numerous physiological, ecological and environmental factors that affect the risks and rewards of anti-predator responses. Birds will return to nests faster if there is a high risk of mortality for unattended nests (Montgomerie and Weatherhead, 1988). In tropical environments where ambient temperatures frequently rise above 41 °C, mortality of embryos can occur in exposed (not shaded by parents) clutches (Bennett and Dawson, 1979; Webb, 1987; Stoleson and Beissinger, 1999).

The type and density of natural predators may also influence optimal return times (Montgomerie and Weatherhead, 1988; Brunton, 1990). Waders may prolong nest return times if there are visual predators such as corvids that can follow waders back to the nests (Weathers and Sullivan, 1981; Martin et al., 2000). Alternatively, if the predominant predators are hedgehogs (Jackson, 2003) or snakes (Weatherhead and Blouin-Demers, 2004) that rely less on visual cues or are opportunistic and hunt only unattended nests, then short nest return times may yield higher hatch success (Bolduc and Guillemette, 2003). Waders may also adjust the length of time engaged in distractive displays because the efficacy (Byrkjedal, 1987) and potential risks may differ among predators (Montgomerie and Weatherhead, 1988).

Parents may also invest more time or energy defending more valuable, older clutches, and thus take a longer time to return to the nest (Montgomerie and Weatherhead, 1988; Brunton, 1990). This age effect on return times may be moderated by the greater vulnerability of exposed older clutches to heat stress (Dawes, 1979; Webb, 1987). Birds may also exhibit stronger parental care for clutches later in the breeding season because they have fewer opportunities to renest within the season and recoup the costs of clutch failure (Barash, 1980; Parish et al., 1997).

Nest return times may also depend on individual nest site (Montgomerie and Weatherhead, 1988) or parental qualities (Conway and Martin, 2000; Gorman and Nager, 2003). For example, nest location could affect the incubation requirements of the developing embryo (Walsberg and King, 1978; Amat and Masero, 2004) and predation risk around the nest (Howlett and Strutchbury, 1997; Martin et al., 2000). Parental qualities that can influence anti-predation tactics include the body condition of the parent (Hegyi and Sasvári, 1998; Dearborn, 2001), as well as previous breeding experience (Montgomerie and Weatherhead, 1988) or habituation to people (Nisbet, 2000).

A bird with high nest attendance (the proportion of time the nest is incubated by either parent) prior to the standardized disturbance may also be likely to quickly return to nests after a disturbance. This is because attendance is influenced by many of the same factors discussed above that shape nest return times (i.e. clutch incubation requirements, parental body condition). Consequently among nests, the individual nest variability in return times are likely to correlate, at least partly, to patterns in nest attendance. For this reason we included nest attendance in our predictive model of nest return times to capture part of the variability in return times due to individuals site or parental characteristics.

In the first part of this study the effects of egg temperature, embryonic age, days into the breeding season, and nest attendance on nest return times were examined. Egg temperature was modeled based on shaded air temperature, cloud cover and time of day, using a thermocouple to predict the temperature inside an exposed similar sized and colored quail egg. To interpret the anti-predation behavior of these plovers and identify predators as well as other sources of disturbances, we monitored causes of nest failure and conducted diurnal predator and disturbance surveys.

The fitness outcomes of different parental anti-predator decisions may depend on physiological or environmental factors that influence the vulnerability of exposed clutches to thermal stress as well as ecological factors such as predation that influence the benefits of distraction displays (Yasué, 2006). In the second part of this study, we examined the relationship between nest return times and hatch success. Previous studies often inferred fitness consequences based on the extent of these behavioral changes without directly measuring changes in productivity or survivorship (Rodgers and Schwikert, 2002; K. Thomas et al., 2003).

In this study we assessed the validity of this approach and also identified conditions in which responses of waders to people could reflect potential costs to fitness.

2. Methods

2.1. Study species

Malaysian plover (*Charadrius peronii*) were selected for this study because previous studies indicated that human disturbance reduces breeding success in related *Charadrius* species (Lord et al., 1997; Weston, 2000; Ruhlen et al., 2003). In addition, no research has examined the ecology or conservation of the Malaysian plover, even though they are near-threatened and there has been substantial growth in beach development throughout their range. The Malaysian plover is a sedentary wader that breeds on beaches in Southeast Asia (Baillie et al., 2004). Biparental incubation begins after the first egg is laid and extends for 25–35 days (Yasué, unpublished data). In the study area the breeding season extends from early April until August (Summer-Smith, 1981).

2.2. Study area

All data were collected on a 40 km stretch of beach in Prachuap Khiri Khan province (12° 05′N 99° 56′E) in the Gulf of

Thailand between 25 April and 25 July in 2004 and 2005. This study area was selected because it is one of the only remaining, relatively undisturbed beaches throughout Thailand with a significant population of Malaysian plovers (Round, unpublished data). Most of the breeding territories consisted of an extensive mudflat (20–400 m exposed at low tide) and a 5–40 m wide beach backed by either mangroves, *Casuarina* trees, *Acacia* scrubland, coconut plantations or abandoned shrimp ponds. The weather from April to May is hot, humid and sunny (diurnal temperature range 28–42 °C). Later in the season the weather is cooler (26–38 °C), cloudier and wetter.

2.3. Nest monitoring

We found nests by searching in areas where pairs were frequently sighted, or by watching birds return to nests. Eggs were floated every one to two weeks to estimate lay date and hatch date (based on 30 day incubation period, Westerskov, 1950), and also detect embryo mortality. Nests were checked every three to five days to assess nest survival and causes of failure. Checks were conducted more frequently close to hatch date because of the high mortality rates of day-old chicks. Predation was assumed to be the cause of nest failure for nests that disappeared between checks, which showed no sign of trampling, inundation, or burial by sand and were more than five days from the predicted hatch date (Yasué and Dearden, 2006b). During nest checks we also resighted adults so that it was possible to differentiate between desertion and predation as causes of failure.

Close to the hatch date, we visited nests every day and recorded the number of peeping or pipped eggs so that it was possible to predict and visit the nest on hatch day. Consequently it was possible to discriminate between nests that were predated before hatch and successful nests in which the chicks died soon after hatch. Behavioral observations of adults and chicks helped determine whether nests had failed or succeeded. Adults with failed nests roosted or fed in pairs on the mudflat, whereas adults with young chicks conducted conspicuous distractive displays when people approached nesting territories. It was also not difficult to count chicks because chicks did not move more than 200 m away from nesting habitats and broods were restricted to a narrow band of beach habitat. Details on non-predation causes of nest failure and responses of plovers to disturbances are presented in a separate study (Yasué and Dearden, 2006b).

Of the 61 and 86 nesting attempts monitored in 2004 and 2005, we observed 73 nests to measure attendance (proportion of time adults incubated or shaded nests). Observations were conducted from a hide or from a seated position more than 100–150 m away from the nest, and lasted for 1–2 h (mean length of observations ± SE = 91.5 ± 4.43 min, total 106 h). At each nest the start and end times of incubation bouts was recorded for both male and female plovers. In addition, shaded air temperature was recorded at a height of 20 cm at the observer's location and percentage cloud cover was visually estimated every 30 min to 1 h. At the end of the nest observation, we recorded the shaded air temperature and percentage cloud cover. These final weather measurements were used in the subsequent models. Imme-diately after recording the weather data, one person then approached the nest by walking directly to the nest at a speed of 50 m/min. Prior to these tests, we used a timer to ensure that disturbance stimuli were standardized and that there was little variability in approach speed. The person disturbing the nest stopped 1 m from the nest for 5 s and then walked back to the hide or viewing location at a speed of 50 m/min. The timer was started when the disturber began to walk away from the nest and we recorded the time taken for adults to return to the nest (seconds). For all trials, it took between 60 and 130 s for the disturber to walk back from the nest to viewing location. At the initial viewing location, we sat down and waited for the bird to return. The birds frequently returned to the nest before the disturber reached initial viewing location. Any replicate disturbance trials were conducted at least 1 week apart on the nest to minimize habituation to standardized disturbance stimuli (Parmelee, 1970; Gochfeld, 1984). It is unlikely that birds responded differently to successive trials due to habituation to our standardized disturbances because birds regularly experienced similar stimuli when local people walked along the mudflat and beaches.

If there was a non-experimental disturbance during disturbance trials, this nest return time was not included in subsequent analysis. If there was a non-experimental disturbance at the end of the predator or disturbance surveys we waited for the plovers to resume incubation for at least 10 min before invoking a standardized disturbance.

2.4. Egg temperature regression model

The egg temperature model was developed by measuring temperature and cloud cover and using a regression analysis to predict temperatures inside similar-sized and pigmented quail eggs (independent samples T test comparison of quail and Malaysian plover egg dimensions: $n_{Quail}/n_{MaPl} = 42/136$, length $t = -1.73$ $P = 0.085$, width $t = -1.80$, $P = 0.082$, mass $t = -1.85$, $P = 0.072$). Although quail eggs were slightly larger (at an α level of 0.10), they were the closest sized eggs available. Three quail eggs were placed inside a recently (within 4 days) disused, Malaysian plover nest cup. First the three eggs were shaded using an elevated cloth plover model that was a similar size and color to a Malaysian plover for 20 min. Then we punctured a small hole in one of the quail egg using a needle and put a 1 mm thick probe from an Omega HHM32 Multimeter Thermocouple into the egg. The sensor was situated near the top surface of the egg, where the embryo is located (Drent, 1975). Then the cloth shading the eggs was removed and the temperature inside the exposed eggs after 1, 2, 3, 5, 10, 15, 20, 25 and 30 min was recorded. At the end of the trial, we measured cloud cover and shaded air temperature using the same methods as during the nest watch. Forty-two trials were conducted over 13 days in 6 different nest cups. We used a multiple regression using shaded ambient temperature, cloud cover, time of day and the square of time of day as predictive variables (to account for non-linear effects, Attrill, 2002). For all subsequent analysis this model was used to estimate egg temperature based on the shaded air temperature, cloud cover and time of day that was measured during nest watches.

2.4.1. Factors affecting nest return times

If we conducted more than one disturbance trial on different days at the same nest, one of the trials was randomly selected for the analysis to avoid pseudoreplication. Thus 73 trials were conducted on 73 different nests. ANCOVA was used to examine the effects of modeled egg temperature, embryonic age, time of day, weeks into the breeding season and attendance prior to the disturbance on return times. In addition it appeared that birds returned to nests slower and spent less time on the nests in the afternoon than the morning, independently of temperature effects. Thus time of day, in two categories (8:00–12:59 and 13:00–18:00) was also included in the model. A binary variable was used instead of a continuous variable because return times varied more between mornings and afternoons rather than by hour. This was visually assessed by plotting 95% confidence intervals of the effect of time of day (hour, 8:00–17:00) on nest return times while controlling for other significant variables. We also included interaction terms between modeled egg temperature and age (days since the start of incubation) because of the age-dependent vulnerability in heat stress for an embryo (Dawes, 1979). The percentage of time plovers spent incubating nests was divided into three categories because the data were strongly negatively skewed. The time taken for birds to return to the nest was log-transformed (base-10) to approximate a normal curve. All five variables and the interaction term were entered into the model. We sequentially removed variables that were insignificant and did not improve the fit of the model.

2.4.2. Predator and disturbance surveys

We recorded any natural or anthropogenic disturbances that occurred during the 106 h of nest attendance observations prior to standardized disturbances. In addition to these surveys, we conducted 241 h of disturbance surveys at 87 nests in the same study area (mean length of observation 80.41 min). For all surveys, we calculated the total amount of time (s) in which plovers left the nest due to the presence of people, dogs, livestock, false alarms and predators. False alarms occurred when plovers responded to a species such as an osprey or curlew that posed no apparent predation risk. Birds were considered "disturbed" if they were exhibiting anti-predatory behavior such as neck out-stretched vigilance posture, flushing onto the mudflat, "rat-running", chasing intruders, calling to distract predators, false brooding or crouching (Gochfeld, 1984). If birds did not exhibit any of these behaviors and simply left the nest, birds were assumed to be switching incubation duties. Usually, the bird leaving the nest would run onto the mudflat to feed or cool its body in tidal pools.

2.4.3. Relationship between nest return times and hatch success

Part of the variability in return times may be influenced by individual nest or bird characteristics. To examine whether these characteristics affected the return times, each nest was identified by a number (nest I.D.) and repeatability measurements were calculated at nests in which we had conducted replicate samples. Repeatability is the proportion of variability among individuals as compared to within individuals (Lessells and Boag, 1987; Gorman and Nager, 2003). Thus this measure indicated the strength of the effect of individual nest characteristics. In addition, repeatability indicates how well the single nest return times measured in 46 of the nests reflected the typical behavior for birds at each nest. Low repeatability suggests that nest I.D. accounted for a very small proportion of the variation in nest return times, undermining the validity of any statistical relationship that may be identified between return times and hatch success. Of the 28 nests with replicate measures, there were 2 trials at 21 nests, 4 trials at 3 nests and 4 trials at 4 nests (total 70 trials).

An ANCOVA was conducted on a subset of the 70 trials, by randomly sampling 1 nest out of each set of replicates for the same nest. Based on this analysis only egg temperature from our regression model, had a significant effect ($P = 0.003$) on nest return times, thus clutch age ($P = 0.945$) and time of day ($P = 0.286$), were not included in further analysis for these 27 nests. The variance component for nest I.D. was then calculated using minimum norm quadratic unbiased estimators (Swallow and Searle, 1978; Sokal and Rohlf, 1981). All 70 trials were included in this analysis and the effect of egg temperature (covariate) was statistically controlled. This variance component was divided by the total variance (within and among group variance) to calculate repeatability. Repeatability was also calculated using the sums of squares method as outlined by Lessells and Boag (1987).

Finally we used binary logistic regression to assess whether return times influenced hatch success. Lay date (Sandercock et al., 1999) and clutch age (Martin et al., 2000) were statistically controlled because both of these factors may influence hatch success in ground nesting waders. The effect of egg temperature was also controlled because in coastal Thailand the fitness consequence of leaving a nest unattended during hot weather is greater than in cool weather. Analyses were run separately for 2004 and 2005 because of the lower hatch success rates in 2005 (Yasué and Dearden, 2006b).

We conducted all data analysis using SPSS Version 11.0 (2001). All r^2 values presented throughout are adjusted values. All error bars represent standard errors. A significance level of $\alpha < 0.05$ (two tailed) was used for all statistical tests.

3. Results

3.1. Predation of nests

Strong winds, frequent rains, and hard substrate around nests limited detection and identification of predator footprints. Predation appeared to account for 30% of nest failure in 2004 (out of 22 failed nests), and 32% in 2005 (out of 47 failed nests). Of the 22 depredated nests there were only four cases in which partial clutches disappeared. Aside from three nests in which broken or punctured eggs were found, eggs disappeared from one check to the next, and there were no remaining signs of the predator (egg shells or foot prints). This suggests that the predators swallowed the egg whole, or carried the eggs away from the nest. As very few predators were observed during surveys, it is possible that nocturnal predators such as snakes (Stake et al., 2005) may have depredated some of the nests. On one morning, we found the tracks of a large snake near a Malaysian plover nest, with plover

tracks weaving back and forth along the snake tracks, indicating that the plover was attempting to lead the snake away from its nest.

3.2. Egg temperature regression model

There was no strong multicollinearity in the independent variables predicted quail egg temperature (Pearson's $r < 0.330$ for all bivariate comparisons, variable inflation factor (VIF) ranged from 1.1 to 1.2, tolerance ranged from 0.82 to 0.89) (Hair et al., 1998). The resulting regression was significant (all independent variables $P < 0.001$, $r^2 = 0.88$). This modeled egg temperature was used in subsequent analysis

$$T_{egg} = -12.86 + 0.906 \times T_{sa} - 0.345 \times C + 3.57 \times H - 0.143 \times H^2,$$

where T_{egg} is the egg temperature, T_{sa} the shaded ambient temperature, C the percent cloud cover and H the time of day (h).

3.2.1. Factors affecting nest return times

Multicollinearity was not a problem because Pearson's r values were less than 0.37, VIF factors ranged from 1.1 to 1.6, and tolerance was between 0.69 and 0.96.

Plovers returned to nests faster when modeled egg temperature was higher (Table 1). Modeled egg temperatures ranged from 30 °C to 46 °C. On cool days, birds followed the disturber away from the nest whereas when egg temperature was very high, plovers often did not follow the disturber and instead ran directly back to the nest after the disturber had passed. Plovers took a longer time before resuming incubation if they had older embryos. Embryo age varied from 0 (lay date) to 40 days. Days into the breeding season had no effect on nest return times. Birds with low attendance prior to the disturbance had longer nest return time and birds returned to nests faster in the mornings than in the afternoons (Table 1).

Although there was no significant interaction term between modeled egg temperature and embryo age when the

Table 1 – Results of ANCOVA showing the factors predicting the return times for Malaysian plovers after a standardized human disturbance ($r^2 = 0.38$, $n = 73$)

Factor	B	df	F	P
Modeled egg temperature (°C)	−0.04	1	7.07	0.010
Embryo age (d)	0.009	1	4.47	0.038
Time of day				
08:00–12:59	−0.25	1	9.52	0.003
13:00–18:00	0.000			
Attendance (%)				
>90	0.27	2	4.44	0.015
69–90	0.29			
<69	0.000			

B is the slope of the line of best fit. The number of days since 1 April ($P = 0.993$), and the interaction between egg temperature and clutch age ($P = 0.368$) were insignificant and so were excluded from the model.

data was split into even-sized temperature categories and an ANCOVA was used to examine the effects of embryo age on return times, age influenced return times at mid ($P = 0.012$) or low temperatures ($P = 0.045$) but had no effect at very high temperatures ($P = 0.662$).

3.2.2. Predator and disturbance surveys

During 347 h of observations, incubating plovers only spent 70 s/h and 48 s/h responding to anthropogenic and natural disturbance, respectively. Out of 343 min in which birds responded to anthropogenic disturbances (76 events), 68, 25 and 8% of the disturbance time were caused by people, dogs and livestock, respectively.

Of the 137 min (21 events) plovers responded to natural disturbances 46, 40 and 15% of the time were caused by false alarms, unknown causes or potential predators. During disturbance surveys plovers distracted one mongoose and three ghost crabs away from nests. Outside of these surveys mongoose, ghost crabs and peregrine falcons were also observed disturbing plovers on four, ten and two other occasions, respectively.

3.2.3. Relationship between nest return times and hatch success

Individual nest or parental characteristics accounted for a substantial proportion of the variation in return times (variance components for nest I.D.: $3.26 \times (10^{-2})$, Error $6.08 \times (10^{-2})$, repeatability = 0.35). Repeatability calculated based on sum of squares (Lessells and Boag, 1987) yielded similar results (0.38).

In 2005, individuals that returned to nests faster after standardized disturbances were less likely to hatch chicks when controlling for days into breeding season ($P = 0.647$), age of
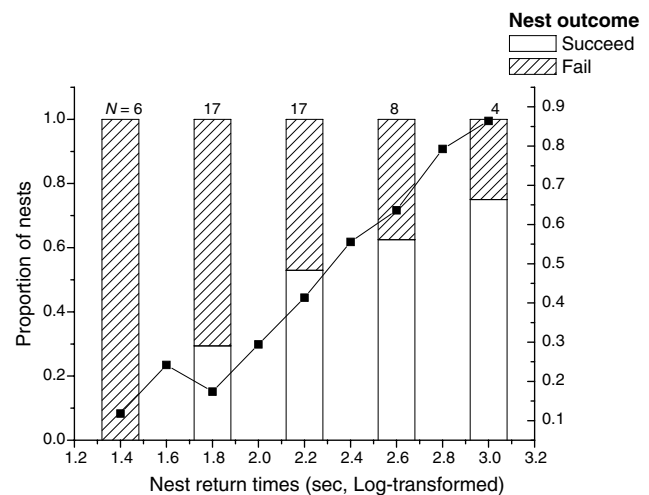

Fig. 1 – Results of binary logistic regression showing the effect of nest return times on the probability of hatching at least one egg for 2005. Stacked bars show the proportion of nests that succeeded (unhatched) and failed (hatched) in each nest return time 0.4 s wide category (location of the bars along x-axis represent medians for categories) and black lines show the predicted probability of success from a model controlling for age of clutch, days into the breeding season and egg temperature.

clutch ($P = 0.696$) and modeled egg temperature ($P = 0.462$, binary logistic regression overall model, $\chi^2 = 12.37$, df = 4, $n = 51$, $P = 0.015$, model coefficients $B = 2.34$, Wald = 5.35, $P = 0.021$, Fig. 1). However, in 2004, nest return time had no effect on hatch success (overall model, $n = 22$, $\chi^2 = 2.11$, df = 4, $P = 0.715$, model coefficient $P = 0.192$) when the same variables were controlled.

4. Discussion

4.1. Factors influencing nest return times

On clear days, modeled egg temperatures often exceeded the optimal incubation temperature range for waders (35–37 °C according to Oppenheim and Levin, 1975; Drent, 1975). The risk of exposing developing embryos to heat stress appeared to limit the amount of time plovers remained off nests after a disturbance. The effect of heat stress on incubation behavior has also been observed in other *Charadrius* plovers breeding in hot environments (Wallander, 2003; Amat and Masero, 2004). On hot days the immediate threat of embryo mortality increases relative to the reduction in predation risk gained by distracting predators and delaying return times. Although temperatures occasionally dropped below optimum incubation temperatures (Drent, 1975; Bennett and Dawson, 1979; Webb, 1987), slight developmental delays due to chilling are unlikely to have a strong effect on breeding success (Norton, 1972) because wader embryos are relatively resilient to cooling and temperatures did not drop below 25 °C during our study (Webb, 1987).

Nest return times were longer for older clutches when accounting for the effect of egg temperature. This is because adults may exhibit longer, more intensive distractive displays as the value of the clutch increases (Regelmann and Curio, 1983; Reid and Montgomerie, 1985). These parental investment factors appeared to be more important than the greater sensitivity to heat stress that has been shown in older embryos of other species (Webb, 1987). However, at very high temperatures, birds always returned to nests quickly regardless of embryo age. This suggests that at very high temperatures the risk of heat stress may outweigh parental investment decisions on nest distractive displays.

Days into the breeding season did not influence nest return times. Malaysian plovers are sedentary species with long breeding seasons compared to temperate or arctic species (Sandercock et al., 1999). Consequently in contrast to previous studies (Skutch, 1949; Martin, 1996), the length of the breeding season may not be a significant constraint on productivity. Plovers were observed renesting up to five times and some pairs were able to fledge more than one brood (Yasué and Dearden, 2006a). In addition, the study period did not continue to the end of the breeding season. Thus it is possible that seasonal changes in return times may be detected if trials were conducted in September near the end of the breeding season.

4.2. Sources of unexplained variation

Despite carefully selecting and testing several variables, the model accounted for only 38% of the variability in nest return times. There may be several other factors such as stochastic changes in predator densities, habituation, or nest microclimates that influence both clutch predation risk and thermal environments illustrating the complexity of interpreting the response of wildlife to people. In a similar multivariate study, 11 out of 16 tested variables influenced incubation behavior and all of these factors together only explained for 57% of the variation behavior (Regelmann and Curio, 1983).

4.3. Predators

Although we attempted to standardize disturbances, the perceived risks were still likely to vary between trials due to the previous experiences of the pair as well as differences in the immediate predator landscape. For example, increased predation risk due to the presence of a mongoose, or habituation due to a large group of people in the vicinity immediately prior to the trial could influence nest return times (Knight and Temple, 1986; Nisbet, 2000).

Compared to other related species, only a small proportion of nests (30–32%) were depredated and few predators were observed (Page et al., 1983; Lauro and Tanagredi, 2002). For these reasons a direct measure of predation risk could not be entered into the model. In other study areas where there is a greater number of visible or detectable predators, the methods used in this study may help to understand the predator landscape in order to improve model predictability (Martin, 1995; Conway and Martin, 2000) and assess the fitness consequences of different nest return times. Future studies focusing on habitat-specific predation risk (Cresswell, 1994; Rodriguez et al., 2001) as well as seasonal or diurnal changes in predation risk may help to parameterize models.

4.4. Nest attendance and return times

Although nest attendance was used to control for individual differences, part of the among-nest variability in return times may not be correlated to nest attendance. For example, a bird in a microsite with high vulnerability to predators may increase bout length to minimize the chance of leading a predator to the nest. In this case, despite greater microsite predation risk, and higher nest return times, overall attendance may not change (Martin and Ghalambor, 1999; Martin et al., 2000). The key factors influencing attendance are the incubation requirements of the nest as well as energetic constraints on the parents ability to incubate (Martin and Ghalambor, 1999). In contrast, nest return times are influenced by these above cost-related factors as well as the perception of risk posed by the approaching human (Gochfeld, 1984). Consequently, differences in risk perception could also cause a mismatch between attendance and return times. Risk perception may depend on the habitat or previous experience of the adult. In addition temperature differences between the period when nest attendance was recorded and immediately prior to the standardized disturbance may have caused slight differences in the incubation requirements of the clutch between the two time periods.

4.5. Egg temperature model

We used a model to predict egg temperatures based on current weather conditions instead of directly measuring egg temperature. We used this approach because this was the first study conducted on this near-threatened species, and we wanted to reduce the amount of time spent around nests using techniques that could disturb birds in a different way than they experience from other forms of non-researcher disturbance. However, measuring more variables that might influence the thermal environment such as vegetation cover around the nest or global solar radiation measurements may have reduced some of the error in the egg temperature model. Moreover, the temperature of the "shaded" quail eggs may not provide the same level of cooling as adult plovers because waders also cool eggs by belly soaking or panting (Ward, 1990; Brown and Downs, 2003).

4.6. Other sources of unexplained variation

Other factors that may account for some of the unexplained variation in nest return times include rainfall, small-scale differences in wind speed around nests (Zerba and Morton, 1983), fluctuations in air temperature and temperature-independent internal incubation rhythms in the parents (Davis et al., 1984). In addition, it is also possible that variable responses to predators between environments or individuals and flexible anti-predatory behaviors may actually be adaptive and help to reduce predation risk in tropical environments where there is a tremendous diversity of predators that warrant different optimal anti-predation strategies (Schall and Pianka, 1980; Weatherhead and Blouin-Demers, 2004).

4.7. Hatching success and return times

In 2005 waders that returned to nests faster were more likely to fail. As waders often respond to broad categories of predators (Gochfeld, 1984), an individual that exhibits strong defensive response to a human may also respond intensely to real predation threats and thus attain higher hatching success (Blancher and Robertson, 1982; Byrkjedal, 1987).

Alternatively, the relationship between hatching success and return times might be a result of differential habitat qualities and territory acquisition abilities (Ens et al., 1992; Byrkjedal et al., 1997). If plovers selected habitats based on microclimate (Walsberg, 1985), the oldest or strongest birds may have secured territories with cooler microclimates and also attained greater success than weaker individuals (Salzman, 1982). Individuals with short return times may also be habituated individuals that are in areas with high non-experimental human disturbance where nests success may be lower. However a concurrent study showed that human disturbance levels in breeding territories did not affect Malaysian plover hatch success in 2005 (Yasué and Dearden, 2006b).

In 2004, nest return times had no significant effect on hatch success. This could be due to different breeding constraints between the years, or lower sample sizes in 2004. Previous studies have demonstrated tremendous inter-year variability in hatch success (Page et al., 1983; Wallander and Andersson, 2003). Factors such as prey availability, weather, changes in the predation environment as well as human disturbance levels may have differed between the two years. Thus long-term studies focusing on habitat or age specific breeding success (Grover and Knopf, 1982; Page et al., 1983) as well as annual variability in nest vulnerability to predation, human disturbance, thermal stress or tidal inundation may help to improve interpretation on the relationship between hatch success and nest return times.

4.8. Conservation implications

This study suggests that longer nest return times do not necessarily indicate greater potential fitness impacts (Stillman and Goss-Custard, 2002; Beale and Monaghan, 2004a). If heat stress on eggs was the only factor affecting nest return times and survival, then nests with greater returns times should have had lower hatch success. However, due to the multitude of factors influencing hatch success and parental behavior, nests with greater return times actually had higher hatch success. Measurements of only nest return times may be an appropriate approach to assess fitness costs of human disturbance in hot environments where heat stress is the dominant cause of nest failure.

Here we demonstrated the value of measuring environmental, ecological and physiological variables that constrain breeding birds, to better interpret a wader's response to human disturbance. Egg temperature, embryo age, attendance and time of day should be measured or controlled in future breeding wader disturbance studies. These variables may influence both the responses of birds to disturbances as well as the fitness consequences of disturbance (Peters and Otis, 2005). As heat stress appeared to be a key factor influencing nest return times, conservation managers should attempt to reduce human disturbance during the hottest periods of the day when behavioral responses appear to be the mildest. Although birds will usually return to nests quickly during these times, they may not do so if the perceived threat is large enough (e.g. a large group of people 2 m from the nest). In our study area, modeled egg temperatures reached lethal levels after only a few minutes of sun exposure. In these cases even short periods of disturbance could impact productivity during hot weather.

Very little is known about wader breeding ecology or impacts of disturbance in the tropics (G.H. Thomas et al., 2003). As far as we know, this is one of the first detailed studies on the responses of tropical waders to human disturbance. A better understanding of the natural constraints as well as the environmental conditions or life history traits influencing the vulnerability of wildlife to human disturbance in the tropics could help researchers identify populations or individuals sensitive to disturbance (Weitzman, 1998).

In general, tropical birds may be more sensitive to human disturbance due to the sensitivity of avian embryos to heat stress (Yom-Tov et al., 1978; Morton and Pereyra, 1985). Moreover, currently, almost half of the red-listed waders breed in tropical habitats. Many of these species such as the Javan plover (*Charadrius javanicus*), or Diademed sandpiper-plover (*Phegornis mitchellii*) are thought to be affected by human

disturbance (Baillie et al., 2004). Tropical waders may be more vulnerable to human disturbance compared to arctic species because of the high human densities on tropical beaches (World Resources Institute, 2004). Although human disturbance is also a pressing issue in temperate environments, in most temperate regions there are now stringent visitor regulations, sign-posted exclosures and well-managed protected areas that reduce the impacts of human disturbance (Mayer and Ryan, 1991; Koenen et al., 1996; Lord et al., 2001; Weston, 2003). In contrast, there are very few examples of these types of conservation strategies in Southeast Asia or in tropical beaches in general.

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